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RECORDS OF THE AUSTRALIAN MUSEUM

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Two New Species of *Exampithoe* Barnard, 1925, Subgenus *Melanesius* Ledoyer, 1984, from Southern Australia (Crustacea: Amphipoda: Ampithoidae)

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ABSTRACT. *Exampithoe (Melanesius) compressa* n.sp. and *E. (M.) halei* n.sp. are described from shallow water in southern Australia. The distinctive compressed body shape sets the former species apart from other *Exampithoe*. *Exampithoe (M.) halei* is of similar body shape as the two previously known species in *Melanesius*, viz. *E. (M.) cooki* and *E. (M.) kutti*, but can be immediately distinguished from them by the angular cutting edge of its gnathopods 1 and 2, and by its vestigial mandibular molar.

JUST, JEAN, 2000. Two new species of *Exampithoe* Barnard, 1925, subgenus *Melanesius* Ledoyer, 1984, from southern Australia (Crustacea: Amphipoda: Ampithoidae). *Records of the Australian Museum* 52(2): 129–136.

Until recently Australian marine ampithoid amphipods had received little attention, although members of the family constitute a diverse and commonly occurring element of the fauna in algal communities and sea-grass beds of subtropical and temperate parts of Australia.

Poore & Lowry (1997) reviewed the status and validity of species reported from Australia, presented diagnoses of all known genera in the Ampithoidae, and described five new ampithoid species, including *Exampithoe kutti* Poore & Lowry, 1997, first Australian record of the genus.

Prior to Poore & Lowry (1997), three species of *Exampithoe* had been described: *E. natalensis* Barnard, 1925 (type-species) from South Africa, *E. gracilipes* Ledoyer, 1984 and *E. cooki* Ledoyer, 1984 both from New Caledonia. Ledoyer (1984) placed *E. cooki* in a new subgenus *Melanesius* based on its lacking a mandibular palp. Poore & Lowry (1997) referred their new species, *E. kutti*, to *Melanesius*.

In the present study two new species of *Exampithoe (Melanesius)* from the south coast of Australia are described. *Exampithoe (Melanesius) halei* n.sp. is similar to *E. (M.) kutti*, while *E. (M.) compressa* n.sp. exhibits an unusual body form.

Unless otherwise stated, left side appendages are illustrated. The length of animals was measured from the mid-dorsal front margin of the cephalon along the dorsal curvature to the apex of the telson.

Exampithoe (Melanesius) Ledoyer, 1984

Diagnosis. See Poore & Lowry (1997).

Description. Cephalon and body strongly to moderately compressed laterally. Cephalon as long as or longer than pereonites 1 and 2 combined, twice as deep as pereonite 1, with moderate to inconspicuous ocular lobes and recession for antenna 2, and wide angled anteroventral corners. Eyes present, round.

Coxal plate 1 as long as or slightly longer than broad, all other plates broader than long. Plates 3 and 4 covering proximal 1/10 of basis of respective pereopods. Pleonal sideplates rounded.

Antennae slender, of subequal length (*E. cooki*: not confirmed).

Mouthparts: Upper lip broader than long, apex entire. Mandibles strongly curved, left and right alike; laciniae mobiles broad, pedunculate, left and right subsimilar, with 5–7 teeth; short (2–3) setal row present. Maxilla 1, inner plate reduced, rounded, with or without a few distomedial setae; outer plate with 10 apical robust setae; palp 2-articulate, extending beyond outer plate, with distomedial to apical setae. Maxillipeds, inner plate with truncate apex, with one short, broad seta apically; outer plate reaching apex of palp article 2, with medial row of robust setae grading into apical and lateral plumose setae; palp 4-articulate with well-developed unguis, unguis with medial row of denticles.

Gnathopods 1 and 2 of subequal structure and size, (gnathopod 1 occasionally broader than 2 in male), with palm convex, defined posteriorly by strong robust seta, distally by smaller, blunt, striated seta (*E. cooki*: striation not confirmed). Pereopods 3 and 4 of equal size and shape, basis strongly inflated, dactylus short, blunt, with large glandular orifice laterally. Pereopods 5–7 of equal shape, 6 and 7 of equal length and longer than 5, article 2 hardly expanded, article 6 with row of robust setae along anterior margin, small oblique grasping palm with straight, smooth or occasionally striated robust setae and one or two curved, blunt, striated robust setae (*E. cooki*: striation not confirmed).

Pleopods slender, peduncle subequal in length to outer ramus, with 2 coupling hooks, rami of equal length (*E. kutti*) or outer ramus about 80% length of inner ramus (*E. cooki*: not confirmed).

Uropods 1 and 2 slender, rami with terminal group of 4 unequally long robust setae. Uropod 3, outer ramus with two recurved terminal robust setae, distally tapering, dorsal surface covered with acute, proximally pointing cuticular scales, inner ramus shorter than outer, flattened, oval, with a few long setae on each side of terminal robust seta.

Telson wider than long to equal width and length, entire, broadest in middle.

Gills present on gnathopod 2 and pereopods 3–6 (*E. cooki*: not confirmed). Gills plate-like, those of gnathopod 2 and pereopod 3 short, linear, of 4–6 longer and broadly oval but of decreasing size.

Oostegites present on gnathopod 2 and pereopods 3–5 (*E. cooki*: not confirmed), oblong oval, densely fringed with long, thin curly-tipped setae.

Key to species of *Exampithoe (Melanesius)*

1 Cephalon and body strongly compressed with cephalon bulging above insertion of antennae 1 ..... *compressa* n.sp.

—— Cephalon and body not compressed, typically ampithoid 2

2 Mandibular molar vestigial. Cutting edge of gnathopods 1 and 2 angular at midpoint between defining robust setae ..... *halei* n.sp.

—— Mandibular molar reduced but distinctive. Cutting edge of gnathopods 1 and 2 evenly curved to nearly straight 3

3 Mandibular molar low, broad, rounded non-triturative with apical setae. Male gnathopod 1 distinctly larger than 2 ..... *cooki* Ledoyer, 1984

—— Mandibular molar low, broad, triturative. Male gnathopods 1 and 2 of similar size ..... *kutti* Poore & Lowry, 1997

Exampithoe (Melanesius) compressa n.sp.

Figs. 1, 2

Material examined. HOLOTYPE: ovigerous female, 6.9 mm, Sellicks Beach, Gulf of St Vincent, South Australia, 35°20'S 138°27'E, *Amphibolis* bed, 7 March 1936, H.M. Hale, Australian Museum, AM P37195. PARATYPES: (38 specimens in all). Same data as holotype, AM P37196 (12). Two Peoples Bay, south-western corner, Albany, Western Australia, 34°57'17"S 118°11'15"E, wash from dense, overgrown *Posidonia* and *Amphibolis* sea-grass, 0.5 m, 28 March 1984, J. Just, Stn AU-25, AM P34815 (1) and P34817 (2). Vancouver Peninsula near Mistaken Island, Albany, Western Australia, 35°04'11"S 117°55'48"E, 6 m, sea-grass with bryozoans (?) or fine pink algae, 13 December 1983, R.T. Springthorpe, Stn WA-120, AM P34818 (23), P34816 (male A).

Description. Cephalon and body extremely compressed; in holotype, ratio of midlateral width of cephalon to midlateral depth = 2 : 5; ratio of width of pereonite 3 level with insertion of coxal plate to lateral depth of segment including coxal plate = 1 : 2. Cephalon bulging above insertion of antennae 1, with strongly convex dorsal curvature, without well defined anterior margin or rostrum. Ocular lobes inconspicuous, rounded truncate. Eyes small, round, about 0.1 mm in diameter.

Coxal plate 1 quadrate; plates 2–5 of increasing size, strongly rounded anteriorly, distinction between large anterior and small posterior lobe in plate 5 poorly defined; plates 6 and 7 small, semicircular, 6 slightly bilobed.

Antenna 1 about 10% longer than 2, flagellum approximately 3 times longer than peduncle, with up to 24 articles, distal ones with aesthetascs; peduncle reaching to apex of or slightly beyond article 4 of peduncle of antenna 2. Antenna 2 with peduncle approximately 70% length of flagellum; flagellum with up to 20 articles.

Mouthparts: Upper lip about twice as broad as long. Mandibular setal row with 3 (left) and 2 (right) short, simple to pectinate setae; molar small, conical, non-triturative, rounded apex scabrous with 1 to 2 small setae; left lacinia mobilis stronger than right. Lower lip with outer lobes rounded, inner lobes roundedly pointed apically. Maxilla 1, rounded inner plates with 1 medioapical seta; palp with apical setae only.

Gnathopods 1 and 2 of equal size and form, with articles 5 and 6 of equal length; cutting edge of 6 weakly convex. Pereopods 3 and 4, article 2 broadly oval, about one and a half times as long as broad, anterior margin with short, posterior margin with long simple setae increasing in length proximally; anterior margin of article 4 evenly convex, not produced apically; articles 5 and 6 slender of equal length, 5 approximately 2.5 times longer than broad, 6 distally tapering, approximately 4 times longer than mid width; dactylus 40% length of article 6. Pereopods 5–7 with narrowly oval article 2, twice as long as broad in 5, 2.5 times longer than broad in 6 and 7, with a few marginal setules anteriorly and posteriorly; articles 5 and 6 of equal length.

Uropods 1 and 2 both reaching to tip of uropod 3. Uropod 1 ratios, peduncle to inner ramus = 3 : 2, inner ramus to outer ramus = 7 : 6; peduncle with few dorsolateral and dorsomedial robust setae and proximal simple setae; inner ramus with one midmedial and 1 distolateral robust setae; outer ramus with 2 lateral robust setae. Uropod 2 ratios, peduncle to inner ramus = 1 : 1, inner ramus to outer ramus = 5 : 3; peduncle with 1 to 2 dorsal robust setae; inner ramus with 1 midmedial and 1 midlateral robust setae, outer ramus with one midlateral robust seta. Uropod 3, peduncle twice as long as middorsal width, with 2 midlaterodorsal setae, dorsoapical margin with a few setae, ventroapical margin with row of approximately 8 unequally long setae; medial robust seta of outer ramus nearly straight, bifid, lateral seta stronger, striate.

Telson length approximately 90% width, roundedly hexagonal, lateral lobes with 2 submarginal long setae, distolateral margins with 3 small plumose setae, dorsodistal surface with 2 long simple setae and 2 tiny cuticular knobs either side of the long setae.

Size. Largest male: 8.9 mm; largest female: 9.8 mm; size range of ovigerous females: 6.9–9.8 mm.

Colour (live animals). Bright green, semitransparent. Eyes shiny ruby-red (AU-25).

Note on behaviour. In the laboratory, specimens from Two Peoples Bay (AU-25) actively sought out *Posidonia* sea-grass blades from a mixture of sea-grasses and smaller algae. Animals would cling to the broad side of the blade in a lateral position. The perfect colour camouflage and the strongly compressed body rendered the animal nearly invisible except for its brilliantly red eye.

Distribution. In sea-grass beds; Gulf of St Vincent, South Australia, and around Albany, Western Australia; 0.5–6 m depth.

Etymology. The species name alludes to the strongly compressed body.

Remarks. The distinctive compressed body shape sets this species apart from other *Exampithoe*.

Exampithoe (Melanesius) halei n.sp.

Figs. 3, 4

Material examined. HOLOTYPE: ovigerous female, 6.3 mm, Port Willunga, South Australia, 35°16'S 138°28'E, H. M. Hale, AM P37197. PARATYPES: same data as holotype, AM P35089 (12) and P37198 (paratype A, male).

Description. Cephalon and body moderately compressed; in holotype, midlateral width of cephalon to midlateral depth = 5 : 6.5; width of pereonite 3 level with insertion of coxal plate to lateral depth including coxal plate = 5 : 7. Cephalon with normal dorsal curvature and front margin; ocular lobes rounded, smoothly integrated into margins above and below. Eyes round, approximately 0.15 mm in diameter.

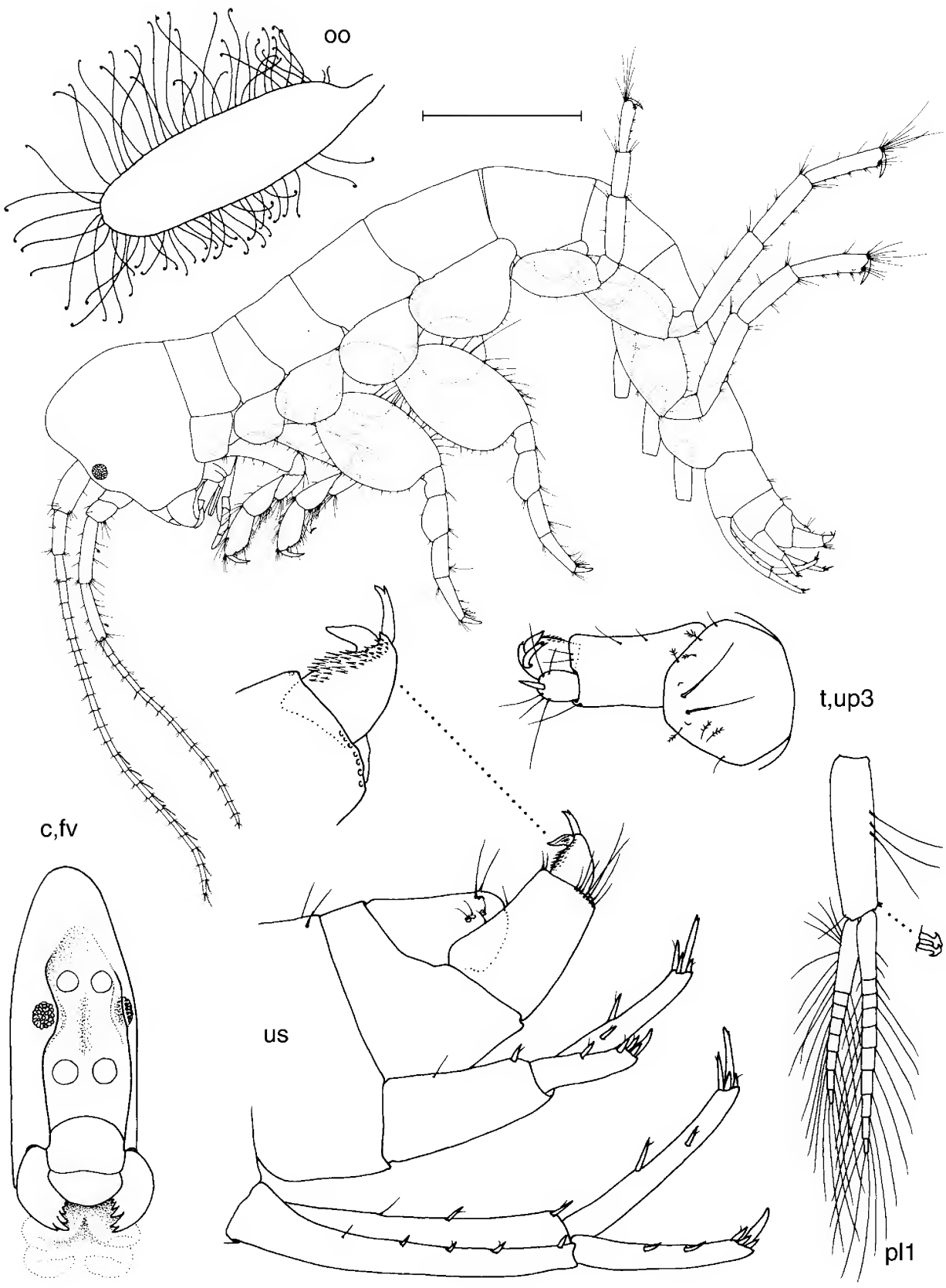

Figure 1. *Exampithoe (Melanesius) compressa* n.sp., holotype. **c, fv**, cephalon, frontal view, insert points of antennae indicated; **oo**, oostegite of pereopod 3; **pl 1**, pleopod 1; **t**, telson; **up 3**, uropod 3; **us**, urosome. Habitus scale bar: 1 mm.

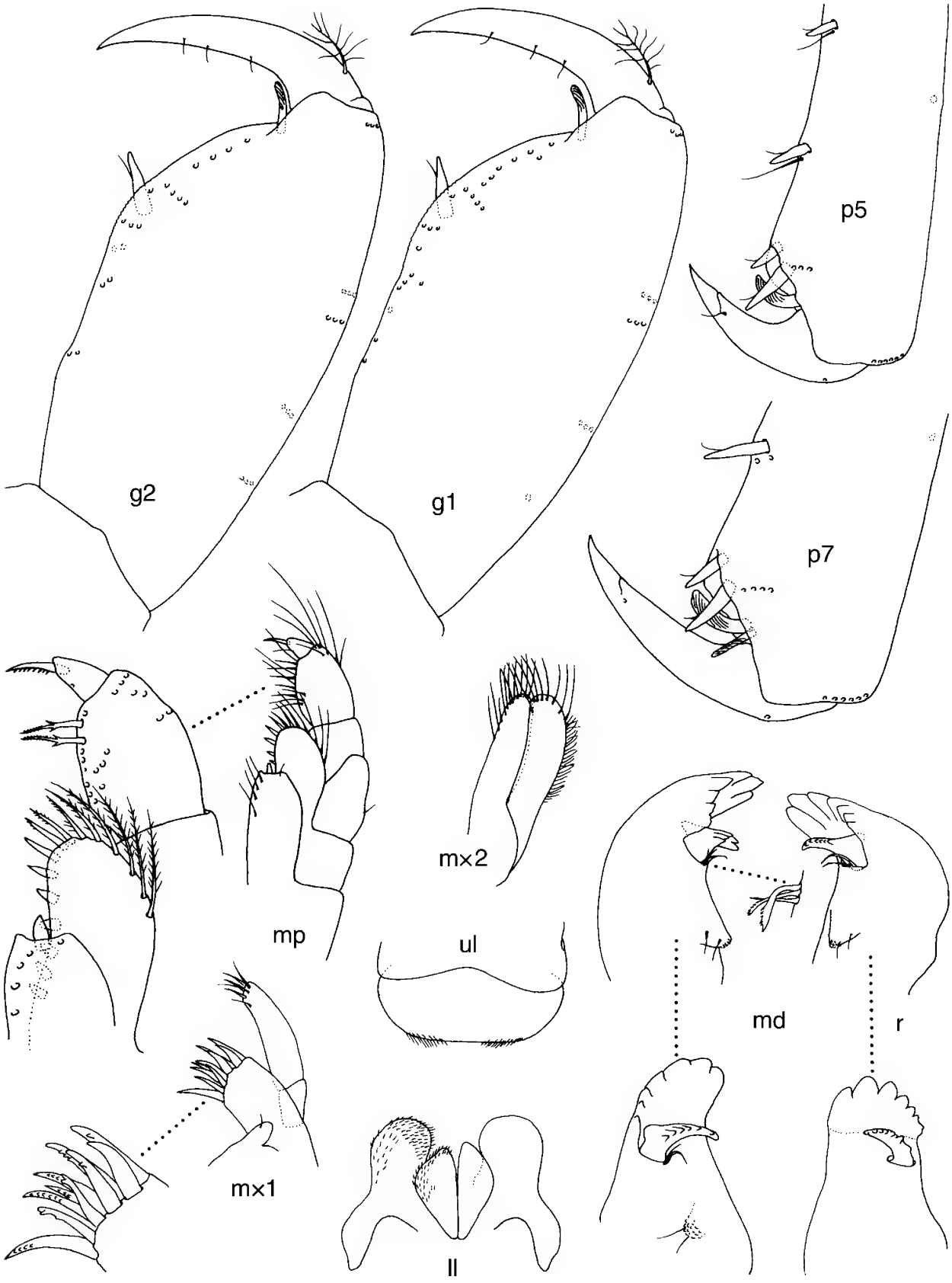

Figure 2. *Exampithoe (Melanesius) compressa* n.sp., holotype. **g**, gnathopod; **ll**, lower lip; **md**, mandible; **mp**, maxilliped; **mx 1**, maxilla 1; **mx 2**, maxilla 2; **p**, pereopod; **r**, right; **ul**, upper lip.

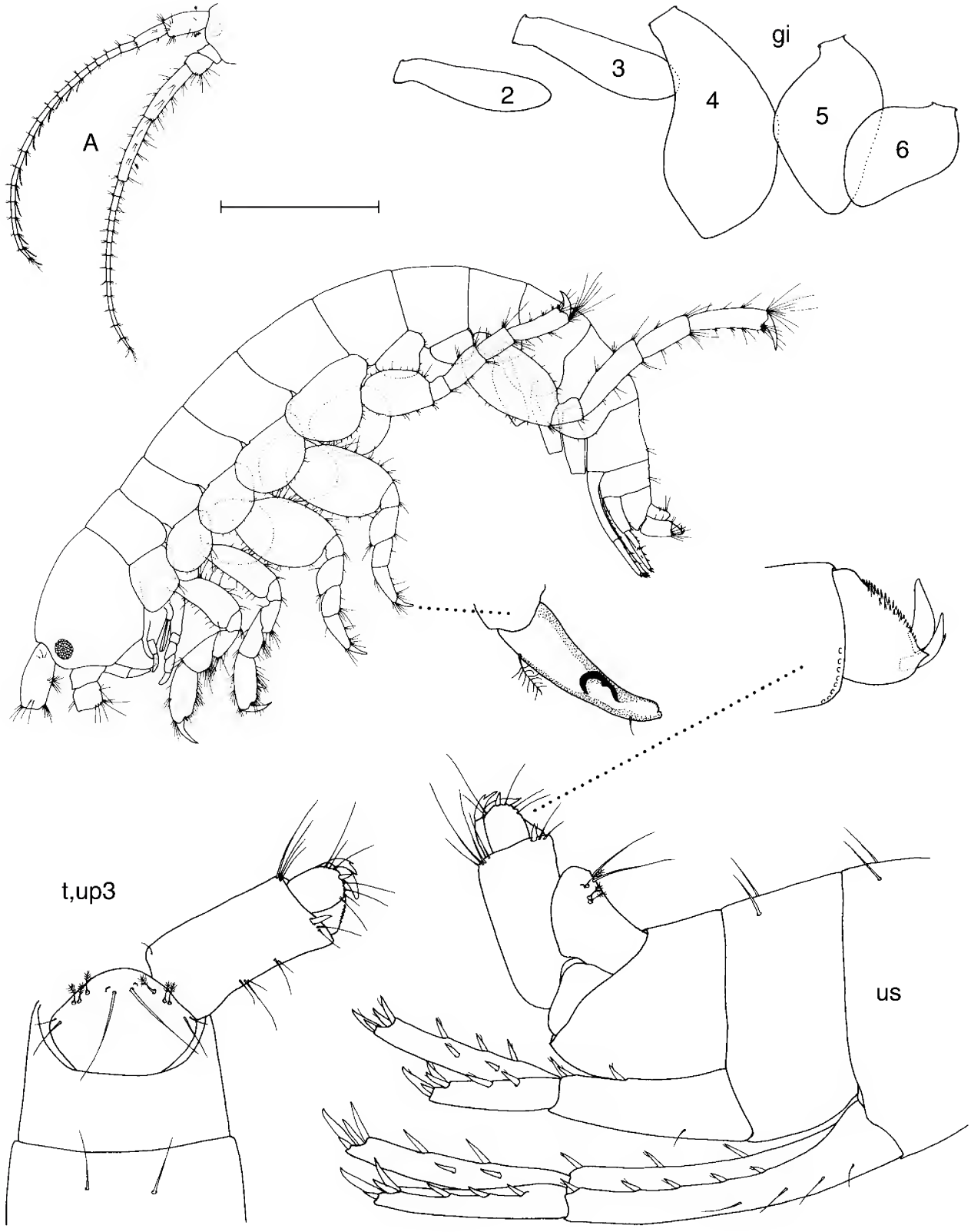

Figure 3. *Exampithoe (Melanesius) halei* n.sp., holotype, except A = paratype A. **gi**, gills of gnathopod 2 and pereopods 3–6; **t**, telson; **up 3**, uropod 3; **us**, urosome. Habitus scale bar: 1 mm.

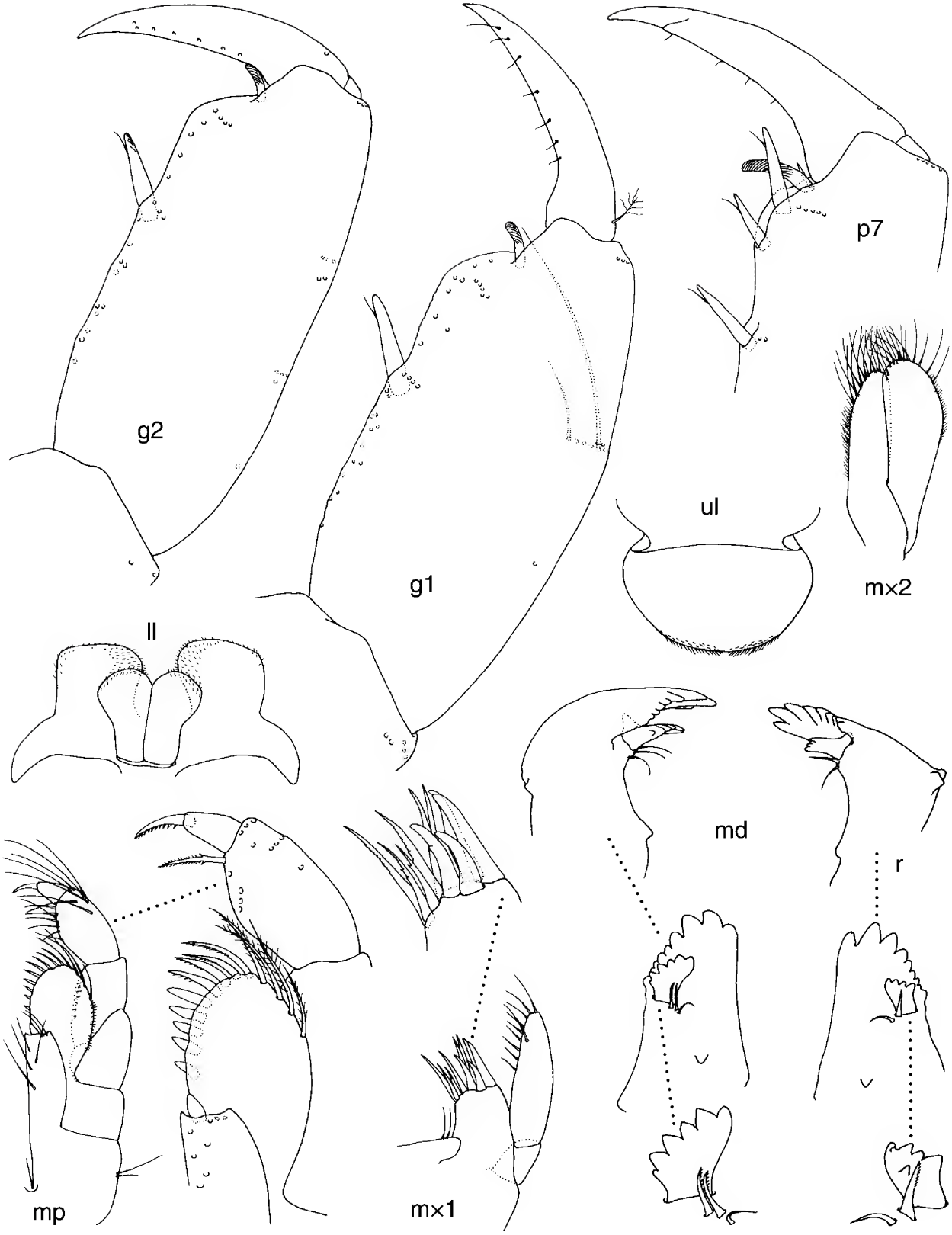

Figure 4. *Exampithoe (Melanesius) halei* n.sp., holotype. **g**, gnathopod; **ll**, lower lip; **md**, mandible; **mp**, maxilliped; **mx 1**, maxilla 1; **mx 2**, maxilla 2; **p**, pereopod; **r**, right; **ul**, upper lip.

Coxal plate 1 near rectangular, anterior margin slightly longer than posterior margin; plates 2–5 of increasing size, strongly rounded anteriorly, 5 rounded triangular with posterior lobe weakly set off from anterior lobe; plates 6 and 7 small, semicircular, 6 slightly bilobed.

Antenna 1 and 2 of equal length. Antenna 1 peduncle 1/3 third length of flagellum, reaching to about the middle of peduncle article 4 of antenna 2; flagellum with up to 24 articles, most flagellar articles with aesthetascs. Flagellum of antenna 2 approximately 10% longer than peduncle, with up to 14 articles.

Mouthparts: Upper lip approximately 50% broader than long. Mandibles with small hump at normal place of palp insertion; setal row with 3 (left) and 2 (right) short, simple to pectinate setae; molar a tiny smooth knob; left lacinia mobilis stronger than right. Lower lip with outer lobes roundedly rectangular, inner lobes rounded distally. Maxilla 1, rounded inner plate with 2 setae; palp with setae apically and along distal half of inner margin.

Gnathopods 1 and 2 of equal shape, articles 5 and 6 of gnathopod 1 slightly larger than in 2, cutting edge of both gnathopods convex, somewhat angular in middle (less so in smaller specimens). Pereopods 3 and 4, article 2 broadly oval, about one and a half times as long as broad, anterior margin with short, posterior margin with longer, irregularly spaced setae; anterior margin of article 4 broadly convex, moderately produced apically; article 5 80% length of 6, width approximately 75% length; article 6 distally tapering, 3 times longer than mid-width; dactylus half the length of article 6. Pereopods 5–7 with article 2 oval, 50% (5) to 70% (6 and 7) longer than broad, anterior and posterior margins with short setae; article 6 40–60% longer than 5.

Uropods 1 and 2 both reaching to tip of uropod 3. Uropod 1 ratios, peduncle to inner ramus = 3 : 2, inner ramus to outer ramus = 7 : 6; peduncle with robust setae along dorsolateral and dorsomedial margins and row of 3–4 simple setae in proximal half of lateral surface; inner ramus with 2 lateral and 2 medial robust setae; outer ramus with 3 lateral robust setae. Uropod 2 ratios, peduncle to inner ramus = 1 : 1, inner ramus to outer ramus = 3 : 2; peduncle with 2 lateral and 1 medioapical robust setae; inner ramus with 3 medial and 2 lateral robust setae; outer ramus with 2 lateral robust setae. Uropod 3, peduncle twice as long as middorsal width, with two middorsolateral groups of setae, dorsoapical margin with 1 robust seta and a few simple setae, ventrolateral apical margin with row of approximately 10 long setae; medial robust seta of outer ramus curved, bifid.

Telson, length approximately 70% width, widest in middle, apex broadly rounded, lateral lobes with 2 submarginal long setae, distolateral margin with 3 small plumose setae, dorsodistal surface with 2 long setae and 2 tiny cuticular knobs either side of the long setae.

Size. Largest male: 5.8 mm; largest female: 7.3 mm; size range of mature females: 6.2–7.3 mm.

Colour and behaviour. Not known.

Distribution. Gulf of St. Vincent, South Australia.

Etymology. Named for H.M. Hale, Australian carcinologist and collector of the present material.

Remarks. *Exampithoe halei* can be immediately distinguished from *E. cooki* and *E. kutti* by its more slender article 6 of gnathopods 1 and 2 and their angular cutting edge, and by its vestigial mandibular molar (*E. kutti*: low triturating ridges; *E. cooki*: rounded, non-triturative projection).

ACKNOWLEDGMENTS. The present study is part of the results obtained during 10 months of field and museum work in Australia (1984) undertaken by the author with support from the Danish Natural Sciences Research Council (SNF 11-4180), the Carlsberg Foundation, Copenhagen, and the Australian Museum, Sydney (AM). R.T. Springthorpe, Australian Museum, kindly provided access to old as well as recently collected, as yet unsorted, material which yielded most of the specimens treated herein.

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A New Species of *Dynoides* (Crustacea: Isopoda: Sphaeromatidae) from the Cape d'Aguilar Marine Reserve, Hong Kong

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ABSTRACT. A new species of sphaeromatid isopod, *Dynoides daguilarensis* n.sp., is described from intertidal black mussel (*Septifer virgatus*) beds in the Cape d'Aguilar Marine Reserve, Hong Kong. This species has been previously misidentified as *D. serratisinus* and *D. dentisinus*. It is characterized by a pleotelsonic apex with an open, sub-parallel slit, both edges of which are serrated from the bottom to the two sides of the apex; uropod endopods which are sub-apically notched externally; and a tubercle on the ventral side of the pleonal process. The composition of *Dynoides* and its relationships to *Clianella* are reviewed. A revised composition of *Dynoides* with a key to the species is provided.

LI, LI, 2000. A new species of *Dynoides* (Crustacea: Isopoda: Sphaeromatidae) from the Cape d'Aguilar Marine Reserve, Hong Kong. *Records of the Australian Museum* 52(2): 137–149.

In this paper, *Dynoides daguilarensis* n.sp. is described from the Cape d'Aguilar Marine Reserve, Hong Kong. The new species is common in the intertidal beds of the black mussel, *Septifer virgatus*. This contribution is part of an ongoing study of the biology—including population dynamics, reproductive biology and behaviour of this species. Because of similarities with other species of *Dynoides*, this species has been wrongly identified in the past. More descriptive information on the species is needed. A key to all species in the genus is also presented.

Dynoides Barnard, 1914

Dynoides Barnard, 1914: 407; Nierstrasz, 1931: 198; Pillai, 1954: 11; Loyola e Silva, 1960: 91; Pillai, 1965: 79, 80; Bruce, 1980: 199, 208, 210; Iverson, 1982: 250; Bruce, 1982: 447; Harrison & Holdich, 1984: 370.

Paradynoides Loyola e Silva, 1960: 101.

Dynoidella Pillai, 1965: 78.

Dynoidella Nishimura, 1976: 275; Bruce, 1980: 199; Iverson, 1982: 250; Bruce, 1982: 447 (non *Dynoidella* Pillai, 1965).

Clianella Boone, 1923: 152; Menzies & Glynn, 1968: 58; Iverson, 1982: 250; Harrison & Holdich, 1984: 363.

Type species. *Dynoides serratisinus* Barnard, 1914.

Generic diagnosis. Cephalon broader than long; mandible with highly-ridged molar process, all pereopods with one strong secondary unguis on the dactyl. Clypeus in inverted V-shape; lobes of labium slightly rounded, distal portion strongly setose. Maxillipeds with 2nd, 3rd and 4th segments of palps inwardly produced. Anterior pereopods without natatory setae, ventral margins more strongly setulose. Pereopodal coxal margins with membrane-like setae. Penes fused along proximal half of length. Appendix masculina elongate, twice as long as endopod, strongly reflexed. Pleon with or without median dorsal process. Pleotelson in form of bilobed dome, convex in centre, flat near margins and apex; apex with variable slit to sinus, notch or foramen, with or without denticulate sides, with or without small inwardly directed, lobe at anterior end projecting into slit. Uropods with both rami broad and lamellar, subequal in length extending some distance beyond pleotelson; exopod folded at right angle to plane of uropod. Ovigerous female with brood pouch formed from three pairs of oostegites arising from pereonites 2, 3 and 4, overlapping well in the midline. Female with exopod of pleopod 3 segmented. Uropods lamellar, not extending beyond pleotelson. Pleotelsonic apex with posterior, simple, rounded dome.

Relationships of *Dynoides* to *Clianella*. The question of whether or not the absence of a pleonal process should be regarded as a critical feature separating *Dynoides* (Barnard, 1914) from *Clianella* (Boone, 1923) has been much discussed.

Harrison & Holdich (1984) argued that the presence or absence of pleonal processes is an important character separating *Dynoides* from *Clianella*, and should be considered a consistent generic character, thereby upholding *Clianella* Boone, with four species: *C. amblysina* (Pillai, 1954), *C. castroi* (Loyola e Silva, 1960), *C. elegans* (Boone, 1923) and *C. globicauda* (Dana, 1853). The only distinguishing character for *Clianella* is the absence of a pleonal process, an apomorphic character state which exists in varying degrees of development in mature males, from absent to elongate (Bruce, pers. comm.). In some species of *Dynoides*, e.g., *D. brevispina* Bruce, *D. brevicornis* Kussakin & Malyutina, *D. saldanai* Carvacho & Haasmann and *D. hoonsooi* Kwon, all of which have a very short, wide or blunt pleonal process or it cannot be termed a process in *D. hoonsooi*. Thus, intermediate stages exist (Bruce, pers. comm.). The ontogenic evidence also suggests that the dorsal process is absent in juvenile males and therefore immature individuals of the two "genera" cannot be differentiated (Bruce, pers. comm.). These two taxa, however, share some unique characters such as a pleotelsonic slit that may or may not have an anterior lobe and internal teeth; a penial process basally fused for half its length and an appendix masculina elongate, twice as long as the endopod and strongly reflexed. Bruce has concluded that the generic name *Clianella* should be suppressed and that *Dynoides*, a genus with an unambiguous definition, should be used for the taxon (Bruce, pers. comm.). *Dynoides* is polymorphic for the pleonal process character.

The author agrees with this interpretation and supports Bruce's conclusions. All species of *Clianella* can be placed in *Dynoides*.

Composition of *Dynoides*. Eighteen species of the sphaeromatid isopod genus *Dynoides* Barnard, 1914 are known to date. *Clianella globicauda* (Dana, 1853) has been placed variously in *Dynamenella* Hansen or *Exosphaeroma* Stebbing (Harrison & Holdich, 1984). Its identity remains unknown (Bruce, pers. comm.), and it is excluded here.

Dynoides amblysinus Pillai, 1954: 11 (**n.comb.** *Clianella amblysina*)—from India.

Dynoides artocanalis Nunomura, 1997: 73—from the intertidal zone of Tachibana Bay, Tokushima Prefecture, Japan.

Dynoides barnardi Baker, 1928: 56—from the coast of New South Wales, Australia.

Dynoides brevicornis Kussakin & Malyutina, 1987: 51—from Furugelm Island, Bochkov Cape, lower horizon of the rocky intertidal among *Laminaria* and *Costaria*; Eastern Cape of Severnaya Bay; Sivuchia Bay, Cape Ostrovok, Falshivigi, Russia.

Dynoides brevispina Bruce, 1980: 119—from Japan (Kwon, 1990: 174) and Korea.

Dynoides castroi Loyola e Silva, 1960: 91 (**n.comb.** *Clianella castroi*)—from Brazil.

Dynoides crenulatus Carvacho & Haasmann, 1984: 23—from the Pacific coast of Mexico.

Dynoides daguilarensis n.sp.—from Hong Kong.

Dynoides dentisinus Shen, 1929: 65—from Peidaiho, China, below low tide mark, Japan (Nunomura & Nishimura, 1976: 21; Bruce, 1980: 200) and Korea (Kwon, 1990: 174).

Dynoides elegans (Boone, 1923: 152) **n.comb.**, (*Clianella elegans*)—from California.

Dynoides harrisoni Kussakin & Malyutina, 1993: 1175—from the intertidal zone of Kat-Ba Island, Gulf of Tonkin, South China Sea.

Dynoides hoonsooi Kwon, 1990: 180—from Korea.

Dynoides indicus Müller, 1991: 313—from a sabellariid reef in Sri Lanka.

Dynoides longisinus Kwon, 1990: 175—from Korea.

Dynoides saldanai Carvacho & Haasmann, 1984: 27—from Puerto Escondido, Pacific coast of Mexico.

Dynoides serratisinus Barnard, 1914: 407—from Shepstone, Natal, South Africa, in the low intertidal.

Dynoides spinipodus Kwon & Kim, 1986: 43—from the south coast of Korea.

Dynoides viridis Bruce, 1982: 447—from Heron Island, Great Barrier Reef, Australia.

A key to the known species of *Dynoides*

Dynoides hoonsooi might be a junior synonym of *D. brevicornis* (Kwon, pers. comm.) and is also excluded from the key. Kwon (pers. comm.) suspects that *D. harrisoni* is a junior synonym of *D. longisinus*, so the name *D. longisinus* is used in this key because of its nomenclatorial priority. This key to species only works for adult males.

1 pleon with elongate dorsal process 2

—— pleon without elongate dorsal process 10

2 pleonal process triangular 3

—— pleonal process not triangular 9

3 pleotelsonic slit with smooth margins, lacking teeth and serrations ..... *D. spinipodus*

—— pleotelsonic slit with teeth, or serrations 4

4 pleotelsonic slit convergent posteriorly 5

—— pleotelsonic slit open to apex 6

5 pleotelson dorsal surface with two rows of distinct tubercles opposite two rows of tubercles on ventral surface of pleonal process ..... *D. barnardi*

—— without these characters ..... *D. dentisinus*

6 pleotelsonic slit anterior end without median lobe but semi-circular proximally ..... *D. longisinus*

—— pleotelsonic slit anterior end with small median lobe 7

7 pleotelsonic slit walls with 3–4 small spines projecting into slit; body bright green, suggesting a green algal habitat ..... *D. viridis*

—— pleotelsonic slit walls more markedly serrate; body not green 8

8 uropod endopod bearing truncate posterior margin ..... *D. serratisinus*

—— uropod endopod with sub-terminal marginal indentation; both edges of pleotelsonic slit with teeth from the bottom to the top ..... *D. daguilarensis*

9 pleotelson dorsal surface with 2 tubercles opposing those on pleonal process ..... *D. brevispina*

—— pleotelson not as above, short pleonal process points upward ..... *D. brevicornis*

10 pleotelson ventral surface having ventilation slit with denticulate margin ..... *D. indicus*

—— pleotelson ventral surface lacking ventilation slit with denticulate margin 11

11 pleotelson surface with two rows of 3 tubercles ..... *D. artocanalis*

—— pleotelson surface lacking such tubercles 12

12 pleotelsonic slit anterior end lacking median lobe ..... *D. crenulatus*

—— pleotelsonic slit anterior end with prominent small median lobe 13

13 body surface setose ..... *D. saldanai*

—— body surface not setose 14

14 pleotelsonic apical notch forming deep narrow slit with smooth lateral margin ..... *D. elegans*

—— pleotelsonic slit denticulate 15

15 uropodal rami margins angular and truncate ..... *D. amblysinus*

—— uropodal rami margins more rounded ..... *D. castroi*

Dynoides daguilarensis n.sp.

Figs. 1–6

Dynoides serratisinus.–Ong Che & Morton, 1992: 220; Kussakin & Malyutina, 1993: 1173 (misidentifications, not *D. serratisinus* Barnard, 1914).

Dynoides dentisinus.–Ong Che & Morton, 1992: 220; Kussakin & Malyutina, 1993: 1173 (misidentifications, not *C. dentisinus* Shen, 1929).

Material examined. Type specimens of *Dynoides daguilarensis* were collected on 7 January 1999, from the black mussel (*Septifer virgatus*) bed which forms a conspicuous mid-littoral, 0.5–1.0 m wide band at approximately mean high water neap tide, i.e., +1.3 m chart datum (Ong Che & Morton, 1992) on the southern shore of the Cape d'Aguilar Marine Reserve, Hong Kong, 22°12.48'N 114°15.67'E. Clumps of *S. virgatus* were removed with a hammer and chisel from the shore, transferred to the laboratory and separated a mussel by washing them with running seawater through a 500 mm diameter mesh-size, metal sieve. The isopods were then separated from other organisms, preserved in 5% neutral formaldehyde, and transferred to 80% alcohol.

Type specimens are deposited in the Australian Museum, Sydney. HOLOTYPE, AM P55943, adult male, bl (body length) 6.5 mm. PARATYPES: AM P55944, adult male, bl 6.2 mm; AM P55945, adult male, bl 5.8 mm; AM P55946, adult male, bl 7.4 mm; AM P55947, adult male, bl 5.6 mm; AM P55948, sub-adult male, bl 4.5 mm; AM P55949, adult male, bl 6.5 mm; AM P55950; ovigerous female, bl 4.8 mm; AM P55951, ovigerous female, bl 4.3 mm; AM P55952, ovigerous female, bl 4.5 mm; AM P55953, sub-adult female, bl 4.1 mm; AM P55954, juvenile, bl 1.8 mm.

Other PARATYPE specimens not dissected: AM P55955, adult male, 1 specimen; AM P55956, sub-adult males, 8 specimens; AM P55957, ovigerous females, 3 specimens; AM P55958, sub-adult females, 6 specimens; AM P55959, juveniles, 58 specimens. The following specimens were collected in 18 April 1999 from the type locality: AM P55960, adult males, 16 specimens; AM P55961, sub-adult males, 12 specimens; AM P55962, ovigerous females, 9 specimens; AM P55963, sub-adult females, 4 specimens; AM P55964, juveniles, 48 specimens.

Other material examined. SWIMS [Swire Institute of Marine Science] CRU-XX171, formerly identified as *Dynoides serratisinus*, 2 adult males, bl 4.7 mm and 4.3 mm, respectively. SWIMS CRU-XX172, formerly identified as *Dynoides dentisinus*, 1 sub-adult male, bl 3.4 mm; 1 ovigerous female, bl 3.5 mm; 1 sub-adult female, bl 3.6 mm; 6 juveniles. These SWIMS specimens collected by Ong Che and Morton in 1992, from the Cape d'Aguilar Marine Reserve, Hong Kong.

Diagnosis. One tubercle produced in ventral side of pleonal process. Antennulae reaching to about eighth joint of flagellum of antenna, to middle of 1st peraeon; flagellum shorter than peduncle. Mandible with highly-ridged molar process, robust and brownish incisor, lacinia mobilis with six spines. Maxillule exopod bearing terminally six spines larger and dark brown, four inner ones slender and serrated; all pereopods with strong secondary unguis on dactyl. Penes distal exterior margin with minute spinules. Pleotelsonic apex with an open, sub-parallel slit and serrated at both edges, extending to bottom of two sides of apex. Endopods of uropods sub-apically notched externally.

Description. Adult male (Fig. 1A,B). Body greatest breadth about half length of body, dorsal surface with dark dendritic chromatophores, but smooth; one orange (freshly collected specimen) curved line in front of and between eyes, anterolateral margins of cephalon produced slightly over narrow transverse furrow when seen from front and with anteromedian portion extended into small process (Fig. 1E). Margin of coxae with setae appearing membranous. Coxae of pereonite 6 reaching not as far back as to overlap lateral parts of pereonite 7. Pleon with posterior margin produced into prominent, triangular, posteriorly pointed, conical process not exceeding beyond anterior end of pleotelsonic slit; sutures of fused pleon not visible. In lateral view, one tubercle produced in ventral side of pleotelsonic process (Fig. 1C).

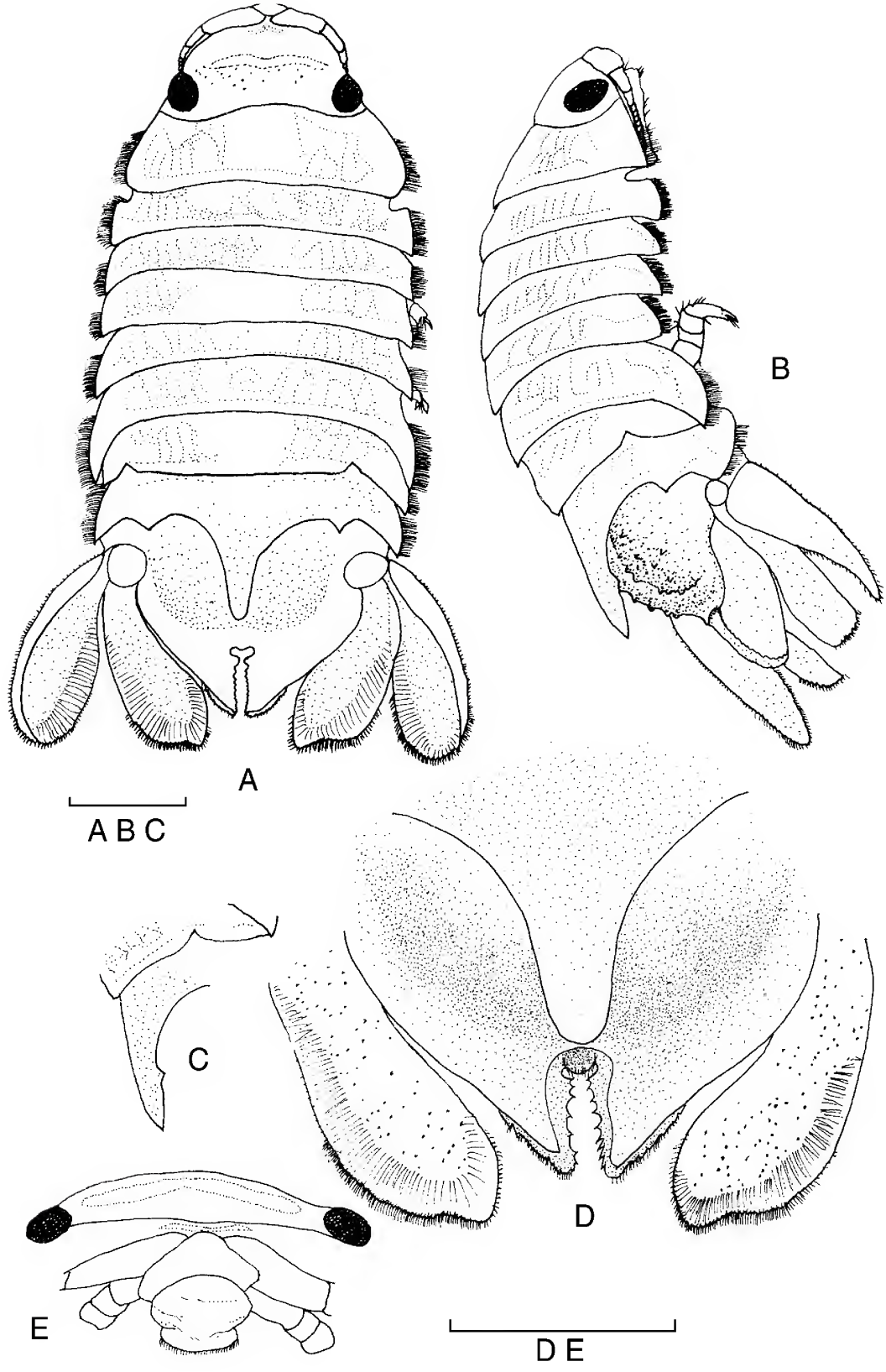

Figure 1. *Dynoides daguilarensis* n.sp. AM P55943, adult male, holotype, bl 6.5 mm. A, dorsal view; B, lateral view; C, pleotelsonic process, lateral view; D, pleotelson, dorsal view; E, head, anterior view including epistome and labrum. Scale bar 1 mm.

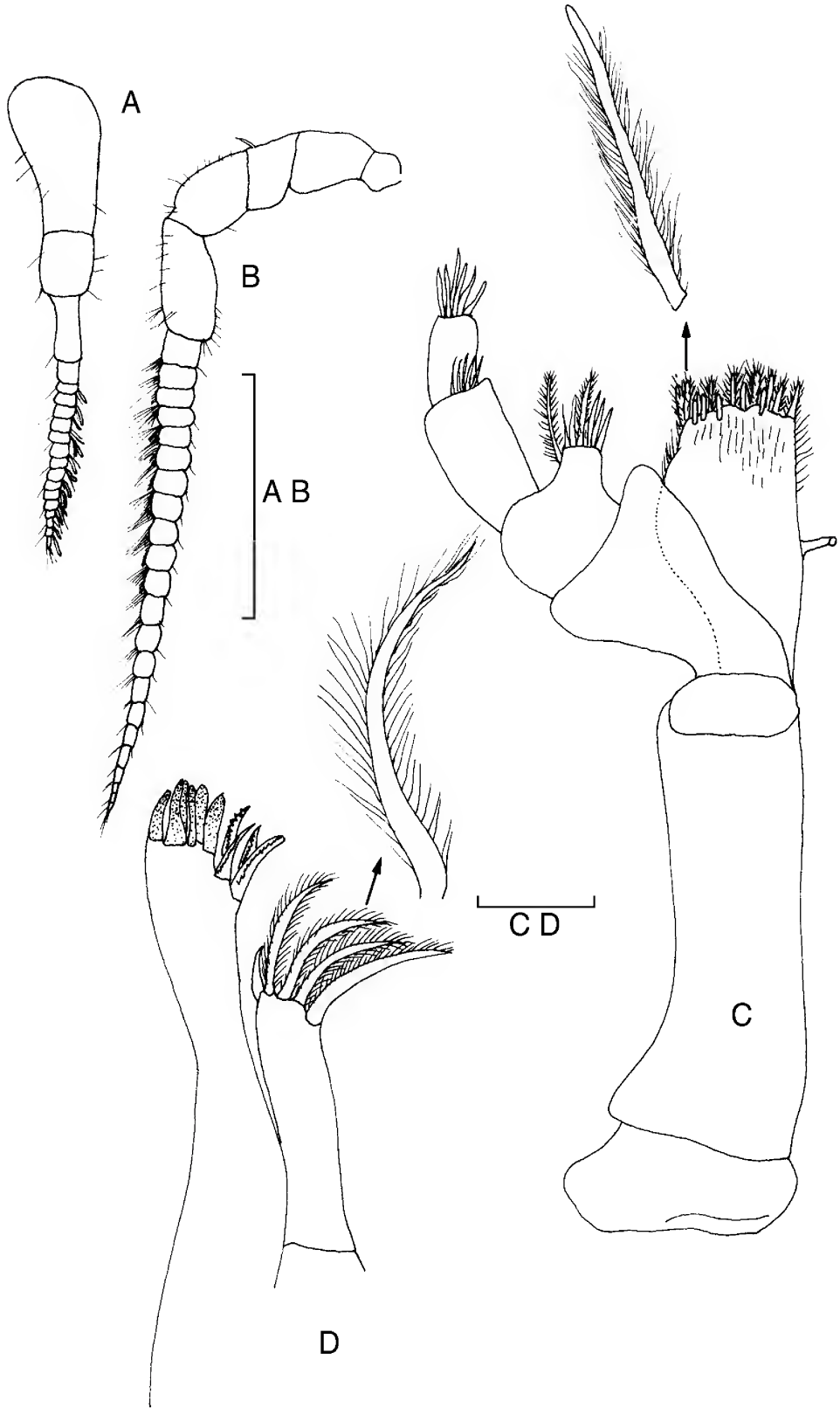

Figure 2. *Dynoides daguilarensis* n.sp. A,B, AM P55944, adult male, bl 6.2 mm; C,D, AM P55949, adult male, bl 6.5 mm. A, right antennule; B, left antenna; C, right maxilliped; D, right maxillule. Scale bars AB 1 mm; CD 0.1 mm.

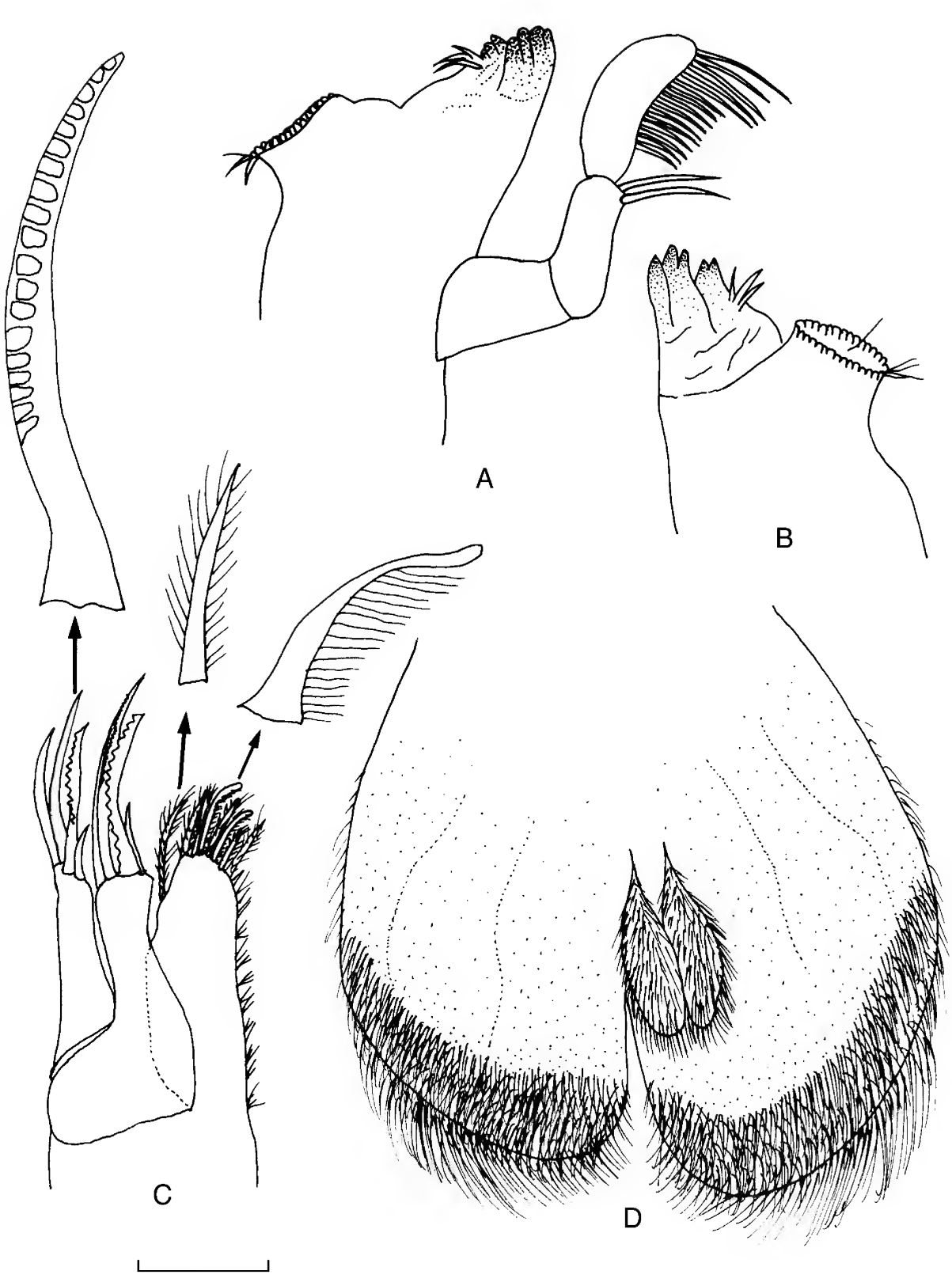

Figure 3. *Dynoides daguilarensis* n.sp. A–C, AM P55949, adult male, bl 6.5 mm; D, AM P55946, adult male, bl 7.4 mm. A, right mandible; B, left mandible, distal part; C, right maxilla; D, ventral view of lower lip. Scale bar 0.1 mm.

Antennule (Fig. 2A). Reaching about antennal flagellum article 8, to middle of pereonite 1; article 1 long, robust and somewhat curved at basal portion, second about half as long as first, article 3 narrower than second; flagellum 16-articulate, each article bearing laterally prominent sensory setae, last article bearing one long seta terminally; flagellum shorter than peduncle.

Antenna (Fig. 2B). Extending to posterior margin of peraeon segment 3; first peduncle article 1 short, article 2 twice as long as 1; combined lengths of articles 3, 4 almost as long as articles 1, 2 combined; article 5 longest, narrowest proximally. Flagellum with 22 articles, setae becoming progressively fewer distally, 1st flagellum article shorter than 3rd peduncle article.

Labrum (Fig. 1E). Almost rounded, setae on free margin; distance from proximal margin to base of labrum about two-thirds breadth across arms, proximal end, each end of arms truncate, sides slightly concave.

Labium (Fig. 3D). Lobes almost rounded, distal portion strongly setose. Two small elongated median lobes situated between them, each setose on surface.

Mandible (Fig. 3A,B). Lacinia mobilis with six spines. Mandibular palp segment 2 bearing two plumose setae on outer distal margin; segment 3 with gradually lengthening plumose setae. Left mandible similar to right.

Maxillule (Fig. 2D). Exopod bearing terminally about ten spines, of which six outer ones larger and dark brown, four inner ones slender and serrate; endopod delicate, with one simple and four plumose setae on terminal margin.

Maxilla (Fig. 3C). Endopod tip bearing about two long pectinate setae and six plumose setae, exopods each bearing about four serrulate spines.

Maxilliped (Fig. 2C). Endite armed with five spines and eight plumose setae on distal margin.

Pereopods (Fig. 6A–C). All biunguiculate and ambulatory, ventral margins more strongly setulose; with one strong secondary unguis on dactyl. Pereopod 1 short, robust; basis and ischium subequal in length; carpus short, about 1/3 length of propodus; basis with some dark chromatophores. Pereopod 2 more slender but longer than first. Pereopod 7 as similar as pereopod 2 in shape.

Penes (Fig. 4F). Long and straight, entirely fused along proximal half of length. Distal exterior margin with minute spinules.

Pleopods (Fig. 4A–E). Pleopod 1 with two coupling hooks on inner margin of peduncle; marginal setae of endopod around 20; one prominent spine present at proximal outer angle of exopod, marginal setae around 23; both ramus with dendritic chromatophores. Pleopod 2 appendix masculina about twice length of endopod, proximal half serrated, distal half slender, flexible and tapering, doubled back on proximal half, marginal setae around 23; exopod marginal setae around 36; peduncle with two coupling hooks. Pleopod 3 peduncle with two coupling hooks; endopod marginal setae around 17; exopod marginal setae around 28 and with simple setae. Pleopod 4 exopod 2-segmented with dark chromatophores. Pleopod 5 with dark chromatophores on surface; two subapical spinulose protuberances present, third one on basal part of inner margin.

Pleotelson (Fig. 1D). Scattered covered with minute tubercles. Open sub-parallel slit, serrated at both edges from bottom to two sides of apex. Teeth on both sides not uniform in shape, distributed asymmetrically, seven teeth on left side, nine on right; one small median lobe on anterior border with setae, projecting posteriorly into slit.

Uropods (Fig. 1D). Extending beyond pleotelson. Endopod sub-apically notched externally.

Colour. Fresh specimens are brown, with bright green or yellow-brown longitudinal median patch on peraeon segments 1–7 and extending onto pleon process.

Body length. 6.5 mm (holotype). Body length ranges between 2.9–7.9 mm (including sub-adult males); numbers of teeth on edges of pleotelson slit are variable from 7–11 asymmetrically.

Sub-adult male (Fig. 4G,H). Pleon with posterior margin produced into short triangular process pointed posteriorly. Pleopod 2 with appendix masculina of same length as endopod, no fold medially, but serrate distally; marginal setae of endopod around 20 and 36 of exopod. (Fig. 4I). Penes very short, minute and separated (Fig. 6I). Pleotelsonic apex with open dome, smooth, both edges not serrate. Uropods smaller, lamellar, not extending beyond pleotelson. Exopod with anterior outer margin folded; endopod not sub-apically notched externally compared to adult males.

Body length. 5.6 mm.

Ovigerous female (Fig. 5A–C). Whole body setose, smaller than male in most individuals; suture in fused pleon visible; three pairs of brood lamellae well developed from pereonites 2, 3 and 4, overlapping in mid-line, brood pouch yellow. Antennae with longer sensory setae (Fig. 6G). Mouthparts all similar to male. Pleon lacks conical median process. Pereopod 1 short, carpus very short and overlapped by strongly produced merus; succeeding pereopod merus moderately produced as compared to pereopod 1 and with one long and strong seta (Fig. 6D–F). Pleopod 3 exopod 2-segmented. Pleopod 5 exopod with 3 spinulose protuberances, 2 subapical and 1 on mediodistal margin (Fig. 5D–H). Pleotelson medially convex, bilobed, with fewer minute tubercles than male, flattened near margins and apex; apex with smooth dome, similar to sub-adult male. Uropods small, never extending beyond pleotelson; endopod longer than exopod; apex of endopod truncate, rounded at exopod.

Body length. 4.8 mm. Body length ranges between 3–5.5 mm.

Sub-adult female (Fig. 5I,J). Smaller than adult female. Peraeopods 2–4 coxae with 3 pairs of triangular oostegite buds. Body surface smoother than adult female. Uropodal exopod shorter than endopod.

Body length. 4.1 mm. Body length ranges between 3–5.5 mm.

Juvenile (Fig. 5K). Uropodal exopod lacking transverse black band.

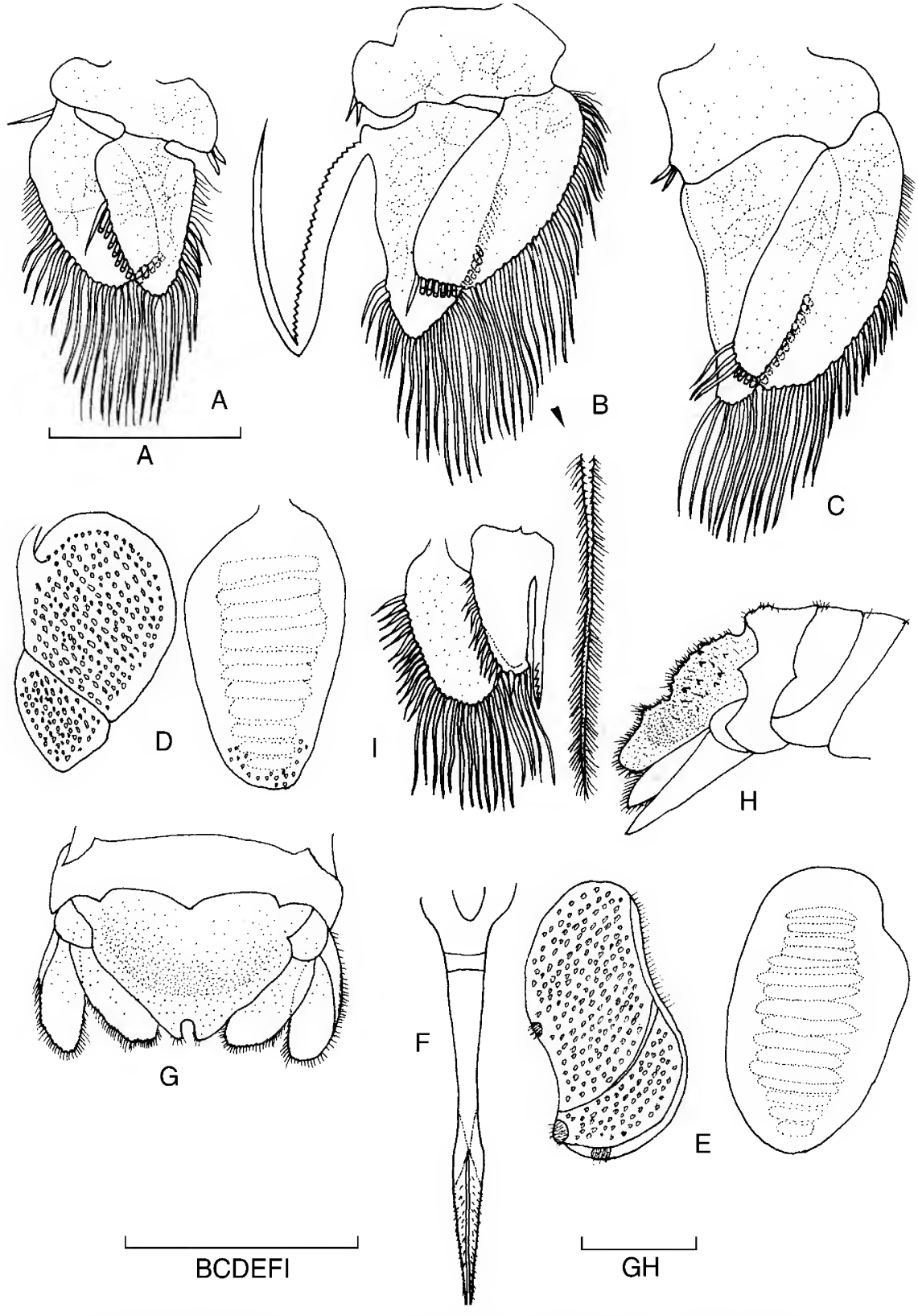

Figure 4. *Dynoides daguilarensis* n.sp. A–F, AM P55944, adult male, bl 6.2 mm; G,H, AM P55947, sub-adult male, bl 5.6 mm; I, AM P55948, sub-adult male, bl 4.5 mm. A, right pleopod 1; B, left pleopod 2; C, left pleopod 3; D, left pleopod 4; E, right pleopod 5; F, penes; G, pleotelson, dorsal view; H, pleotelson, side view; I, pleopod 2 with appendix masculina. Scale bars 1 mm.

Body length. 1.8 mm. Body length is generally less than 3 mm. Manca length ranges between 0.9–1.5 mm. Freshly collected juveniles occur in a variety of colours and ornamental patterns on the dorsal surface.

Remarks. This species is easily distinguished from most other described species of *Dynoides* by its pleotelson tip having a parallel-sided slit decorated with teeth and a median lobe at the anterior end. The only other species with these characters is *Dynoides serratisinus* Barnard, 1914, but the pleonal process and uropod differ in the two species. In *Dynoides daguilarensis*, the pleonal process has a tubercle on the ventral side, the pleotelsonic slit edges are serrated from the bottom to the two sides of the apex. The uropodal endopod apex is not truncate as in *D. serratisinus*, but has a sub-terminal, marginal indentation. Additionally in *Dynoides daguilarensis*, the antennule flagellum is shorter than the peduncle and the apex of the inner plate of the maxilliped is not rounded as in *D. serratisinus*. Furthermore, in *D. serratisinus*, Barnard (1914) described a seventh joint in all pereopods with 3 lamella-like teeth, and Kensley (1978) reported that the tubercles on the telson are sharp, neither of which is the case in *D. daguilarensis*.

Kussakin & Malyutina (1993) recorded specimens of *Dynoides serratisinus* Barnard, 1914 from the Cape d'Aguilar Marine Reserve, Hong Kong. These authors were uncertain of the identity of this species and only focused on the parallel-sided slit of the pleotelson, but neglected the morphology of the posterior body parts, e.g., the numbers of teeth on the edges of the slit and their asymmetrical arrangement. The inner ramus of the uropod was not truncate but with a sub-terminal marginal indentation instead. These are the key characters that differentiate *D. daguilarensis* from *D. serratisinus*.

Kussakin & Malyutina (1993) also recorded *D. dentisinus* Shen (1929). There is little doubt that the record is a sub-adult of *D. daguilarensis* with a developing short pleonal process. Furthermore, their specimen was collected from the type locality of *D. daguilarensis* in Cape d'Aguilar. However, during the present three year study period, *D. dentisinus* has not once been collected from Hong Kong. *Dynoides dentisinus* Shen may be distributed in more temperate waters, as previously reported, such as northern China, Korea and Japan. In Japan, beds of *Septifer virgatus* are the habitat of *D. dentisinus* (Iwasaki, 1996).

Ong Che & Morton (1992) reported upon two species of *Dynoides* from the *Septifer virgatus* community at Cape d'Aguilar, Hong Kong, i.e., *D. dentisinus* and *D. serratisinus*. Examination of their material shows that the ecological information they recorded relates to *D. daguilarensis*.

Etymology. This species' name refers to the type locality—Cape d'Aguilar, Hong Kong.

Discussion

Habitat and distribution. *Dynoides daguilarensis* lives on intertidal rocky shores, commonly in association with beds of the black mussel *Septifer virgatus*, which is present year round at Cape d'Aguilar. This dense mat supplies the isopods with food, a means of escaping desiccation, immersion and predation, protection from wave action and a permanent, stable, refuge. The *Dynoides daguilarensis* population at Cape d'Aguilar spends its entire life cycle in the mussel beds. It can, however, also be found in the empty tests of the barnacle *Tetraclita squamosa squamosa*, among clumps of the stalked barnacle *Capitulum mitella* and is associated, seasonally, with the algae *Dermonema frappierii, Pterocladia tenuis, Chaetomorpha antennina* and *Ulva fasciata*, all characteristic biota of wave-exposed shores in Hong Kong.

In Hong Kong, this isopod is not restricted to the type locality, but has been found from Shek O and Big Wave Bay on Hong Kong Island, and also in beds of *Septifer virgatus*. Both localities are on the southeastern coastline of Hong Kong, where wave action is strong and oceanic, and where the environment is less polluted (Morton, 1989). *Dynoides daguilarensis* is absent from the western regions of Hong Kong, where the salinity is lower (Morton & Morton, 1983), ranging between 6.0 and 33.5‰ (Chiu, 1998), whereas in the southeast the salinity ranges from 20–35 ‰ (Morton & Wu, 1975). Because the shore is more sheltered than in the east, no *S. virgatus* is present and *Dynoides daguilarensis* has not been recorded. This species appears to have a habitat preference for exposed rocky shores experiencing strong wave action, oceanic waters and a relatively unpolluted environment and is always associated with the mussel *S. virgatus*.

Population biology. Data on *Dynoides daguilarensis* collected from March 1997 to January 1999 at four sites in the Cape d'Aguilar Marine Reserve, indicates that three separate peaks of recruitment occurred, producing spring, summer and late autumn cohorts. Individuals were sexual active year round and gravid females occurred in all months. Juveniles were released continuously and were always more abundant than adults over the course of the year. *Dynoides daguilarensis* was more abundant during the warm months from spring to early winter (April and May to December) and declined during colder months from winter to early spring (January to April). During the warmer months, isopods grew and matured faster but to a smaller size whereas in the colder months they grew at a slower rate but to a larger size.

The eggs of *Dynoides daguilarensis* are yellow, nearly round and 0.3 mm in diameter. Newly hatched mancas were 0.9 mm long, 0.5 mm wide and sexually indistinguishable. The body was bright yellow, semi-transparent with a pair of dark compound eyes. No movement was observed other than body contractions. A week after hatching, black dots of pigment occurred on the body surface and movement commenced. Mancas tended to swim at the water surface and were distinctly photopositive. A positive relationship between the size of ovigerous females and brood size (r =

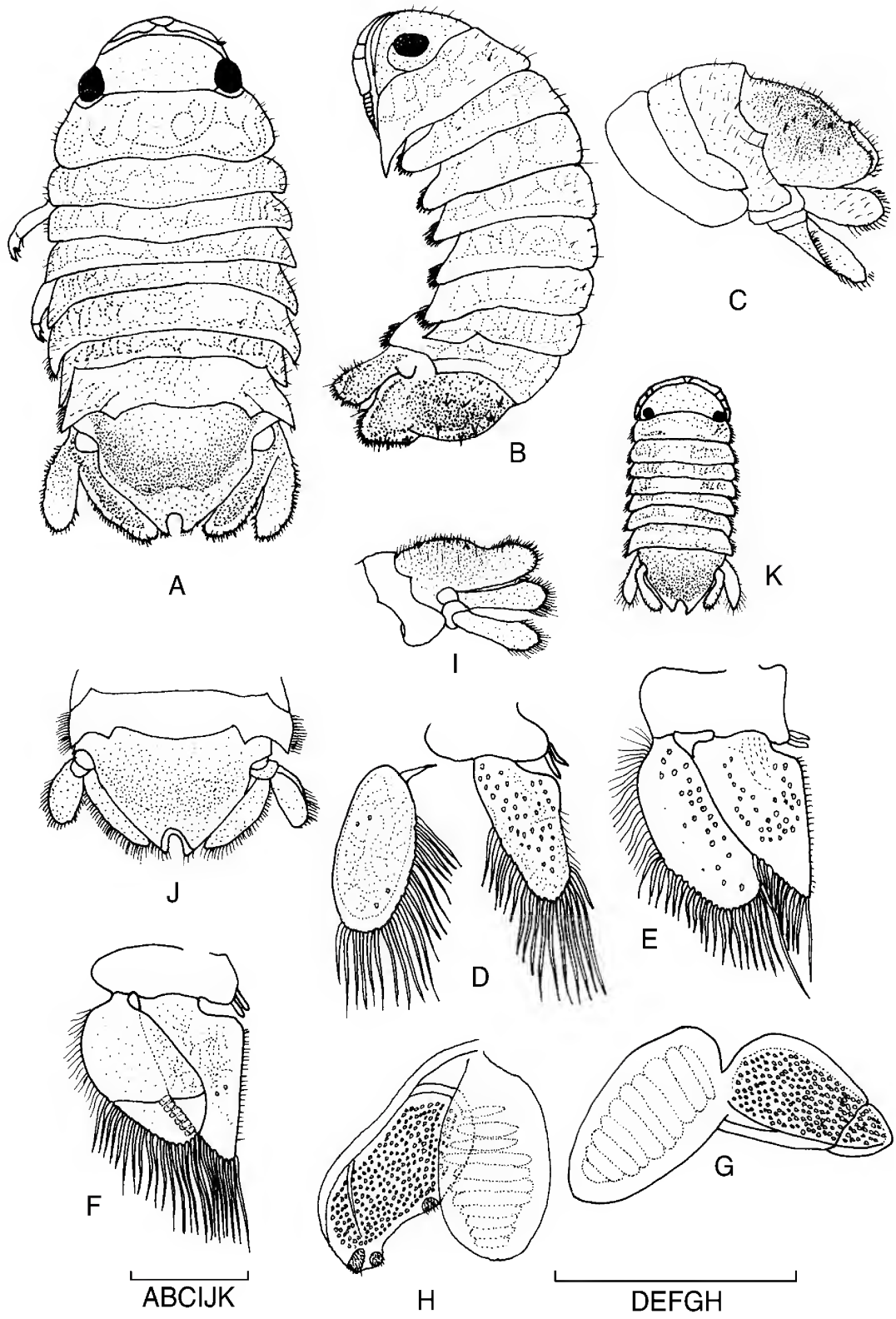

Figure 5. *Dynoides daguilarensis* n.sp. A–C, AM P55950, ovigerous female, bl 4.8 mm; D–H, AM P55951, ovigerous female, bl 4.3 mm; I,J, AM P55953, sub-adult female, 4.1 mm; K, AM P55954, juvenile bl 1.8 mm. A, dorsal view; B, side view; C, pleotelson, side view; D, left pleopod 1; E, left pleopod 2; F, left pleopod 3; G, left pleopod 4; H, left pleopod 5; I, pleotelson side view; J, pleotelson dorsal view; K, dorsal view. Scale bars 1 mm.

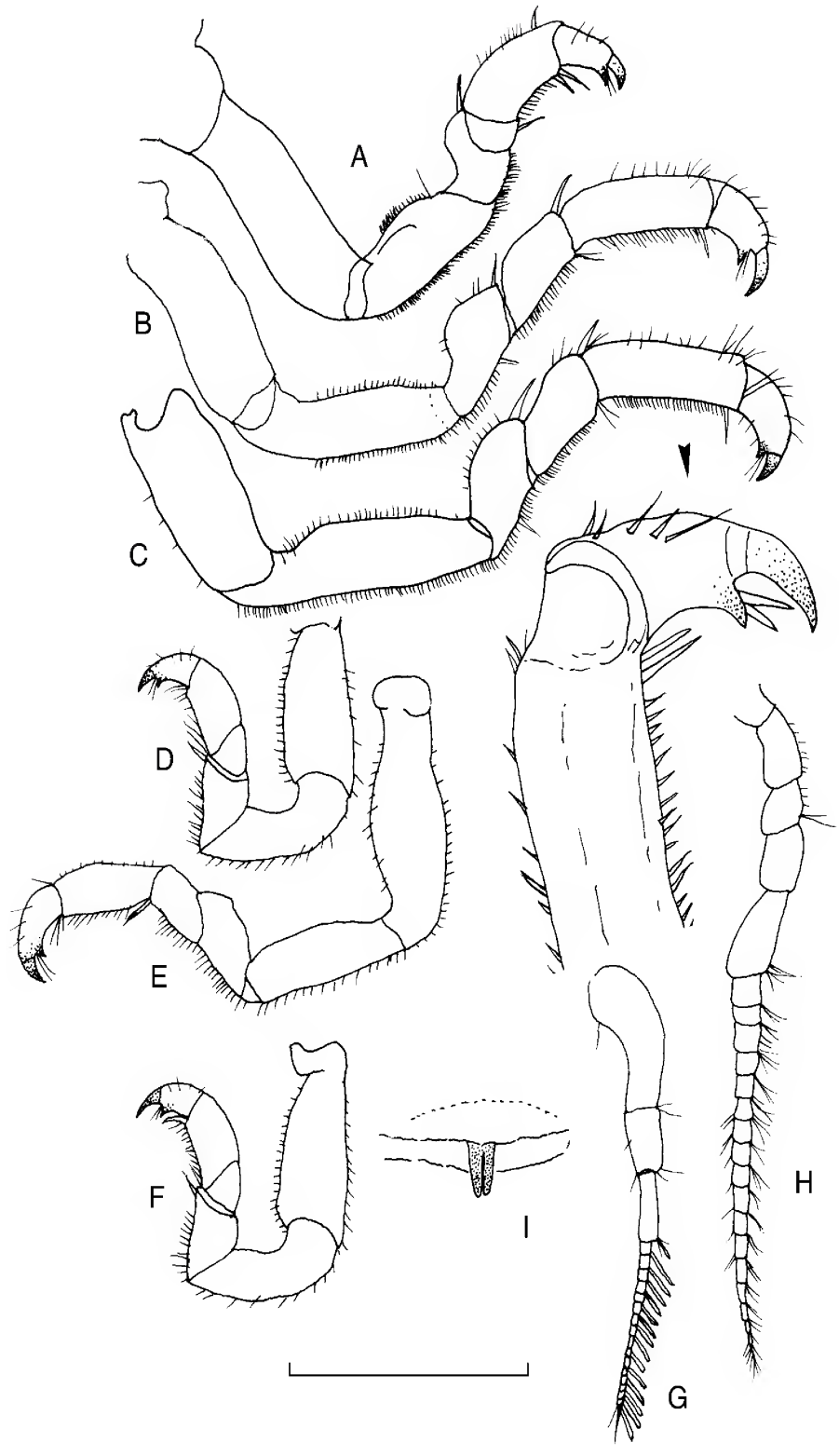

Figure 6. *Dynoides daguilarensis* n.sp. A–C, AM P55945, adult male, bl 5.8 mm; D–F, AM P55952, ovigerous female, bl 4.5 mm; G,H, AM P55951, ovigerous female, bl 4.3 mm; I, AM P55947, subadult male, bl 5.6 mm. A, pereopod 1; B, pereopod 2; C, pereopod 7; D, pereopod 1; E, pereopod 2; F, pereopod 7; G, left antennule; H, left antenna; I, penes. Scale bar 1 mm.

0.57, $p<0.001$) was observed. The number of brooded eggs or juveniles, significantly increased with increasing parental size, regardless of season. The brood size ranged from 26 to 56 eggs per brood (Li, 2000).

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A New Genus and Species of Athericidae (Diptera: Tabanoidea) from Cape York Peninsula

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ABSTRACT. The new athericid *Suraginella macalpinei* n.gen., n.sp. is described on specimens from the Claudie River and Jardine River systems in the north of Cape York Peninsula. This distinctive taxon is compared with the widespread Old World genus *Suragina* Walker, 1858, to which it has some misleading resemblances. Many differences are detailed between these genera. In the closure of wing cell m_3, and in having dorsal setae on certain radial and cubito-anal veins in the female, *Suraginella* resembles the rare monotypic Brazilian genus *Xeritha* Stuckenberg, 1966. Although these conditions are apomorphies, they are considered unreliable for cladistic analysis. A survey of the occurrence of such setose veins in other Athericidae and in the sister-group Tabanidae shows them to be sporadic, variably developed, and probably subject to homoplasy. No sister-group of *Suraginella* can be identified. The presence of a hard, dark mass in the abdomen of half of the available females indicates with high probability that *S. macalpinei* takes bloodmeals from a vertebrate host. A test of gut contents for the presence of blood, using urological test strips, gave a strong positive result but is not conclusive. Biological considerations suggest that *Suraginella*, although occurring in both "tip-of-peninsula" and "mid-peninsula" rainforest regions of Cape York Peninsula, may be independent of the forest biome. The preferred range of the aquatic larval stages in river profiles may determine distribution. Present information suggests that *Suraginella* may be part of the old "autochthonous" element in Australia.

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The Australasian Athericidae have not been the subject of any study since the monograph by Paramonov (1962) on the Rhagionidae (= Leptidae). At that time, Athericidae had not been distinguished from the Rhagionidae as a separate family; this distinction was made by Stuckenberg (1973) and is now generally accepted. Paramonov's monograph dealt only with the fauna of continental Australia and Tasmania. He thus excluded those species of the athericid genus *Suragina* Walker, 1858, also classified then as rhagionids, which had been described from the Indonesian (Maluku) section of the Australasian Region (see Nagatomi & Evenhuis, 1989). The only athericid genus recorded by Paramonov was *Dasyomma* Macquart, 1840. A species named originally as *Atherix pusilla* Macquart, 1858, based on a specimen from Adelaide, was transferred to the widespread rhagionid genus *Chrysopilus* Macquart, 1826.

Dasyomma is the only athericid genus with a southern Gondwanan distribution, occurring in both mainland Australia + Tasmania and Chile + Argentina—an AS group in Hennig's (1960) terminology. It was considered by Stuckenberg (1973) to be a sister-group to all other athericids, and was segregated in its own subfamily, the Dasyommatinae (originally named incorrectly as Dasyomminae). The 11 named species recorded by Paramonov are limited to montane habitats with running water suitable for the aquatic larvae. Six species occur in New South Wales (two of them in the ACT), four in Tasmania, and one in the southern extremity of Western Australia. A specimen from the Atherton Tableland of northern Queensland was not named, although it probably represents a twelfth species.

The presence of another athericid taxon in Australia was revealed when Colless & D.K. McAlpine (1970) recorded an unnamed "*Atherix*" in the textbook *The Insects of Australia*. In response to my enquiry about this, Dr David McAlpine sent me the small series on which this record was based. At that time, the generic classification of Athericidae was relatively undeveloped and *Atherix* was a general repository for species of uncertain affinity. I established that the specimens probably represented a new genus and species of the subfamily Athericinae. Study of these interesting flies had then to be deferred, but in the long intervening period many additional specimens were collected. A fresh examination based on all available material now confirms the identification of a new genus and species, herein named *Suraginella macalpinei* n.gen., n.sp.

Material and methods

The specimens are dried, pinned flies in the collections of the Australian Museum, Sydney, and the Department of Zoology and Entomology at the University of Queensland, Brisbane, and in the collection of G. Daniels of Brisbane. Standard morphological terminology is used; the naming of wing veins follows J.F. McAlpine (1981). Nomenclature of thoracic features follows the description and illustrations by Stuckenberg (1973). Details of hypopygial structures and female mouthparts were obtained from specimens macerated in hot KOH and mounted in glycerine jelly after dissection. Wing length was measured from the distal end of the basicostal scale. Thoracic length was measured from the anterior margin of the mesonotum to the posterior edge of the scutellum as seen in dorsal view. Overall length of females was not measured as their abdomen is always irregularly curved. Overall length of males excludes antennae. T = tergite, S = sternite. Label data are cited as originally given; a slash (/) indicates the end of a line of printing on a label.

Systematic description

The flies at first sight seemed to be of a strange, unusually small species of *Suragina*, a genus not yet recorded in Australia. Close study, however, revealed many differences; to bring these out, a detailed comparison with *Suragina* is made in the following generic description.

Suraginella n.gen.

Type species. *Suraginella macalpinei* n.sp.

Etymology. Diminutive of *Suragina*—suggested by the superficial resemblance of these small athericines to the considerably larger species of that genus; feminine.

Diagnosis. Relatively small athericines with unusually short abdomen, broad and strongly patterned wing, and distinctive appearance due especially to conspicuously banded abdomen; cell m_3 closed; anal lobe sexually dimorphic, broader in ♂; T1 not divided in midline in either sex; ♀ wing with setae dorsally on R_{4+5}, basal part of R_5, and all of CuA; gonostyle with prominent elongate extension at base; ♀ vertex sunken, ocellar tubercle close to upper extremity of frons and not visible in lateral view; ♀ frons without velvety-black pruinescence over upper section.

Description

Male. *Head*. Flattened in longitudinal axis, much broader than long; eyes very close together over most of length of frons, narrowly separated by a distance less than width of anterior ocellus, diverging only slightly towards ocelli, diverging over a short distance above antennae and enclosing small, subtriangular frons which has a transverse impression; frons with shifting, silvery-grey pruinescence over entire length, lacking setae; ocellar tubercle partly visible in lateral view, situated a short distance anterior to upper eye corners; antennae set very low; parafacials entirely inclined towards face, not visible laterally; genae not visible laterally; face deeply recessed, hidden in lateral view; palps slender, strongly arched; proboscis distinctly shorter than head height (Fig. 1). [In *Suragina*, frons usually very narrow over upper section and tapering towards ocelli over most of its length due to gradual convergence of eye margins, appearing slightly biconcave because of curved eye margins; lower triangular portion of frons above antennae extending more extensively upwards; frons at narrowest clearly less than transverse width of anterior ocellus; lower frons usually with distinct setae; ocellar tubercle prominent in lateral view, situated relatively further forwards and posteriorly enclosed by a patch of shining pruinescence; face small but visible in lateral view; proboscis relatively longer, more slender, than in *Suraginella*.]

Thorax. Relatively less elongated than in *Suragina*; postmetaspiracular scale well formed, flat; suprametacoxal pit of typical athericine form; metapleural epimera visibly extended to midline of venter and uniting behind metacoxae. Fore and middle legs slender; fore tarsus with long setae below; fore claws and pulvilli highly asymmetrical, inner claw short, slender, pointed, slightly curved, outer claw much larger, strongly curved, flattened, apex rounded; outer pulvillus enlarged, like a leaf partly curled longitudinally, darker brown than inner pulvillus and with narrow dark border; tibial spurs 0.2.2, posterior spur of middle leg reduced, less than half length of anterior spur. Hind leg: coxa with pale knob on anterior face, and pale, bluntly

rounded apical spur; femur laterally flattened except basally, of almost uniform width throughout, a shallow groove impressed over apical half of anterior face; tibia (Fig. 1) strongly flattened, with pronounced longitudinal groove over most of length of anterior and posterior surfaces, in lateral view tapering moderately towards base, slightly narrowed apically; tarsomeres relatively stout, basitarsus longer than tarsomeres 2–5 together, entire tarsus appearing almost cylindrical with only slightly decreasing diameter apically. Femora with many long setae; all tibiae with abundant, small, dark, stiff, suberect setae; hind tibia with prominent fringe of long, dark, stiff setae on dorsal surface, on ventral surface a dense fringe of much shorter setae. Femora 1 and 2 of about equal length in both sexes, tarsus 3 about 1.1 × length of tarsus 2 in both sexes; tarsus 1 about 1.3–1.4 × length of tibia 1 in both sexes [in all these proportions resembling *Suragina*]; femur 3 about 1.7 × length of femur 2 in ♂. [In *Suragina*, all legs appear to be more slender and elongate; hind femur and tibia moderately flattened, also with longitudinal groove on flattened surfaces, and fringed dorsal and ventral surfaces; tibiae with very small, stiff, dark setae but these usually depressed, except on ventral surface of tibia 1 where they are erect.]

Wing (Fig. 1). Relatively short and broad, broadest basally near basal end of large anal lobe, apex moderately rounded; alula and lower calypter large. Cell m_3 closed at margin or with short stalk. R_4 gently sinuous and ending at or just anterior to wing apex; M_3 markedly arched where it forms posterior border of discal cell. Radial and cubito-anal veins without rows of erect setae dorsally. [In *Suragina* the wing distinctly more elongate; cell m_3 nearly always open, if almost closed then this condition usually unstable; discal cell more elongate and closer to wing margin, apical section of M_3 about half, sometimes less, of the preapical section forming posterior border of discal cell; greatest width of wing across its middle, and anal lobe more rounded. Veins R_{4+5}, R_5 and CuA without setae in both sexes.]

Abdomen. Proportionately short (Fig. 1), relatively slender, not wider than thorax; T1 with prominent anterior projection on each side of deep median depression, short behind this depression but without median notch in hind margin and not divided or weakened in midline; T2–5 all of about equal length, T6 and T7 shorter, T8 only about half of length of T7; S1 reduced to a narrow, transverse, asetose band not clearly distinct from S2; S7 elongate, and as long as T7+8, enabling hypopygium and S8 to be flexed dorsad into vertical posture. [In *Suragina* the abdomen more elongate, tapering progressively from T1 where it is widest; basal excavation in T1 proportionately smaller, subtriangular; T1 not divided in midline by a weakness or break in sclerotisation; sides of basal depression in T1 continue anterolaterally into anteriorly-directed humps which are relatively shorter and more transverse than in *Suraginella*; S1 a short, strongly transverse, asetose band.]

Hypopygium. Epandrium, gonocoxites and cerci with long setae. Hypopygium (Fig. 4) broad, gonocoxites relatively short with arched lateral margins, joined ventrally by a narrow, sclerotised band constituting basal margin; inner ventral side of each gonocoxite arches inwards basally and terminates in a medially-directed point, a narrow, finely setose, transverse area of membrane separating the two points from the band. Gonostyles (Fig. 5) remarkable in form, having a finger-like extension from base of the almost straight, quite slender main component, which expands apically into an irregular ovoid form with a preapical narrowing. Parameral sheath broadly subtriangular; two short, stubby points preapically on each side, one ventrolateral which is reflexed, and a lateral one which curves posterolaterally and is bluntly rounded; apex with fringe of stiff microsetae; tines strongly curved dorsad; ejaculatory apodeme broadly expanded, strongly keeled in midline; gonocoxal apodemes diverging as illustrated. Epandrium (Fig. 6) broadly subovate, cerci short and bluntly rounded.

Female. *Head*. Narrow in lateral view (Fig. 2), longest axis of eye almost vertical, much of eye surface located on anterior face with facets facing forwards; parafacials only very narrowly visible (sometimes not visible) in lateral view, genae not visible or only very narrowly so. Frons (Fig. 3) virtually parallel-sided over entire length, narrow, at midlength about one-fifth of greatest head width, smooth (without median ridge or furrow), shining apruinose over broad median section, lateral borders narrowly pruinose. Ocellar tubercle not visible in lateral view as vertex is slightly sunken, area behind tubercle curving immediately into occiput; ocelli almost in equilateral triangle, lateral ocelli placed close to upper eye margins. Antennae situated low, only narrowly separated from eye margin, first segment short, subannular, second segment a little longer, third segment subreniform, narrow above, somewhat flattened on ventral edge; style dorsal, slender, microsetose. Face deeply inset, small, dorsal bordering suture deeply impressed; in profile its anterior margin shallowly rounded, upper surface quite flattened; face projecting obliquely anteroventrally, clearly visible between palps in lateral view. Palps extended forwards, strongly arched on upper surface, slightly arched below, tapering to narrow apex, deepest near base; upper surface without setae, occupied by a sensory field of closely-packed chemoreceptor sensilla, elsewhere with stiff, brown setae. Proboscis stout, relatively short, less than height of head; stylets reaching to apex of labella. [In *Suragina*, ocellar tubercle further forwards on frons, lateral ocelli distant from upper corners of eyes by about length of tubercle; ocelli prominently visible in lateral view; eye usually more rounded in lateral view, but this condition variable between species; suture bordering face not so deeply impressed; dorsal margin of face more rounded in profile, not flattened; proboscis longer and more slender; palps chevron-shaped, strongly arched on both dorsal and ventral surfaces; extensive part of upper frons velvety-black.]

Thorax. As in ♂; legs generally as in ♂, apical spur of metacoxa elongate and pointed; femur 3 about 1.3–1.5 × length of femur 2 [1.5–1.8 × in *Suragina*, intraspecifically variable].

Wing. Venation as in ♂; erect setae in row dorsally on R_{4+5}, basally on R_5, and on entire length of CuA; wing form sexually dimorphic, in ♀ anal lobe more gradually rounded,

hence not as broad. [In *Suragina* no setae present dorsally on veins mentioned; no sexual dimorphism in shape of anal lobe, or this very slight.]

Abdomen. Proportionately short, only slightly longer than thorax, maximum width at posterior margin of T2, about equal to width of thorax; T1 with roughly square, median basal depression which extends to hind tergal margin, this tergite produced anteriorly on each side into a broadly subconical projection, no median notch in hind margin or midline desclerotisation; T2 is longest tergite, T3 and T4 subequal, T5–7 progressively shorter and more transverse, T8 very short, only narrowly exposed, cerci very shortly exposed; S1 very narrow, bare. [In *Suragina* the basal depression relatively smaller, shallow, broadly subtriangular, short longitudinally and more distant from hind tergal margin; abdomen widest over T1; T1 divided in midline by a narrow longitudinal strip of pale, weakly sclerotised integument, hind margin often with shallow notch in midline.]

Suraginella macalpinei n.sp.

Figs. 1–6

Etymology. Named in honour of the distinguished Australian dipterist, Dr David McAlpine.

Type material. HOLOTYPE ♂: [Queensland] Bertie Ck [Creek], 1 km SE / Heathlands H.S., Qld / 11°45'S 142°35'E / 23 Mar 1992 / G. Daniels, M.A. Schneider [in Queensland Museum, Brisbane, No. T57819]. PARATYPES: 17 ♂♂, 5 ♀♀, same data; 5 ♂♂, 2 ♀♀, Jardine R. Cape York / Pen. N.Qld / 11°08'S 142°35'E / 14 Oct. 1979 / M.S. & B.J. Moulds [G. Daniels Collection, Brisbane]. 1 ♂, West Claudie R. / Iron Range N. Qld. / 20 Sep. 1974 / M.S. Moulds; 2 ♂♂, Middle Claudie R. / Iron Range N. Qld. / 22 Sep. 1974 / M.S. Moulds; 1 ♂, Martin Creek / S. of Iron Range / N. Qld. / 24 Oct. 1974 / M.S. Moulds; 3 ♀♀, Claudie R. near / Mt Lamond, N. Qld. / 28 May 1966 / D.K. McAlpine; 1 ♀, Claudie R., 1 mile / W. Mt. Lamond, Qld. / 13 Dec. 1971 / D.K. McAlpine / G.A. Holloway / D. P. Sands.

Description

Male. *Head*. Upper section of frons dull yellowish-brown in frontal view, lower section dark brown; entire frons and parafacials silvery-grey pruinose, colour shifting; antennal scape brown, pedicel and postpedicel pale yellow, all with thin, shifting, silvery pruinescence; scape with short, dark bristles dorsally, pedicel fringed on outer apical edge with dark bristles; stylus very slender, brown. Face dark brown, thinly silvery pruinose. Palps dull yellowish-brown, paler on dorsal sensory area, with stiff, brown setae. Proboscis brownish with dark setae. Ocellar tubercle very dark brown, a group of stiff, erect setae posteriorly. Occiput shining silvery-grey, dorsally with dark velvet mark along eye margin, and with many shining white hairs. Genae with long brown hairs.

Thorax. Mesonotum dark brown, paler areas on humeral calli, postalar calli and transverse sutures; quite densely covered with shifting greyish pruinescence; scutellum dark brown, similarly pruinose, with many fine, brown setae. Pleura mostly dark brownish, pteropleuron more yellowish-brown; membranous area around anterior spiracle dull parchment yellow; mesopleuron with fine, soft, white hairs, sternopleuron bare; pleura generally with thin, shifting silvery-grey pruinescence, less evident on paler parts. Fore legs: coxa and femur pale amber-yellow, coxae darker brown on outer surface, with fugitive silvery pruinescence; femur fringed with long, dark, suberect hairs dorsally, some long hairs below and on posterior surface; tibia and tarsus with dense, small, suberect, brownish setae; tibia brown, tarsus darker brown. Middle legs: coxa brownish, with dark, bristly hairs anteriorly; femur amber-yellow, a poorly defined brown zone basally, with fine, brownish setae; tibia darker amber-yellow, with very small, dark setulae. Hind leg: coxa brown like adjacent pleura; femur bicolorous, whitish-yellow on a little less than basal half, brown apically, with many shining, brownish setae, these longer on upper surface; tibia and tarsus shining brownish, with strong, dark vestiture.

Wing. Strong smoky-brown pattern (Fig. 1), stigma darker brown, costal cell weakly brownish tinged; hyaline areas as illustrated. Halter knob dark brown, stem basally yellowish-brown.

Abdomen. Conspicuously bicolorous, appearing strongly banded; T1 entirely brown, T2 entirely dull yellowish, T3 dull yellowish transversely across short anterior section, remainder brownish, T4 like T3, other tergites and hypopygium brownish; all tergites with numerous, erect, dark setae.

Measurements. Body length 6.0–6.5 mm; thorax length 2.0–2.3 mm; wing length 5.8–6.4 mm.

Female. *Head*. Frons shining blackish-brown, bordered laterally by narrow strip of pale, silky-yellow pruinescence; silvery-grey pruinescence above antennae and on parafacials, and some small, pale, porrect setae; ocellar tubercle with dark, erect bristles of irregular length; otherwise as in ♂.

Thorax. Pronotum and humeri pale brownish-yellow; transverse sutures yellow-brown, elsewhere the mesonotum dark brown with some reddish tinting; fine, shifting, ashy-grey pruinescence present, denser behind humeri and over prescutellar area and on anterior border of scutellum. Legs and wing pattern as in ♂.

Abdomen. Strongly banded as in ♂; T1 blackish-brown except warm golden-yellow on posterior border; T2 entirely golden-yellow, with some brownish tinge (probably due to postmortem changes in gut contents); T3 dark brown, except narrowly yellow along anterior border; T4 like T3 but not as dark and with an obvious paler area medially; remaining tergites dull brownish; vestiture pale, shining on T2, brown elsewhere.

Measurements. Thorax length 1.7–2.5 mm; wing length 6.0–6.9 mm.

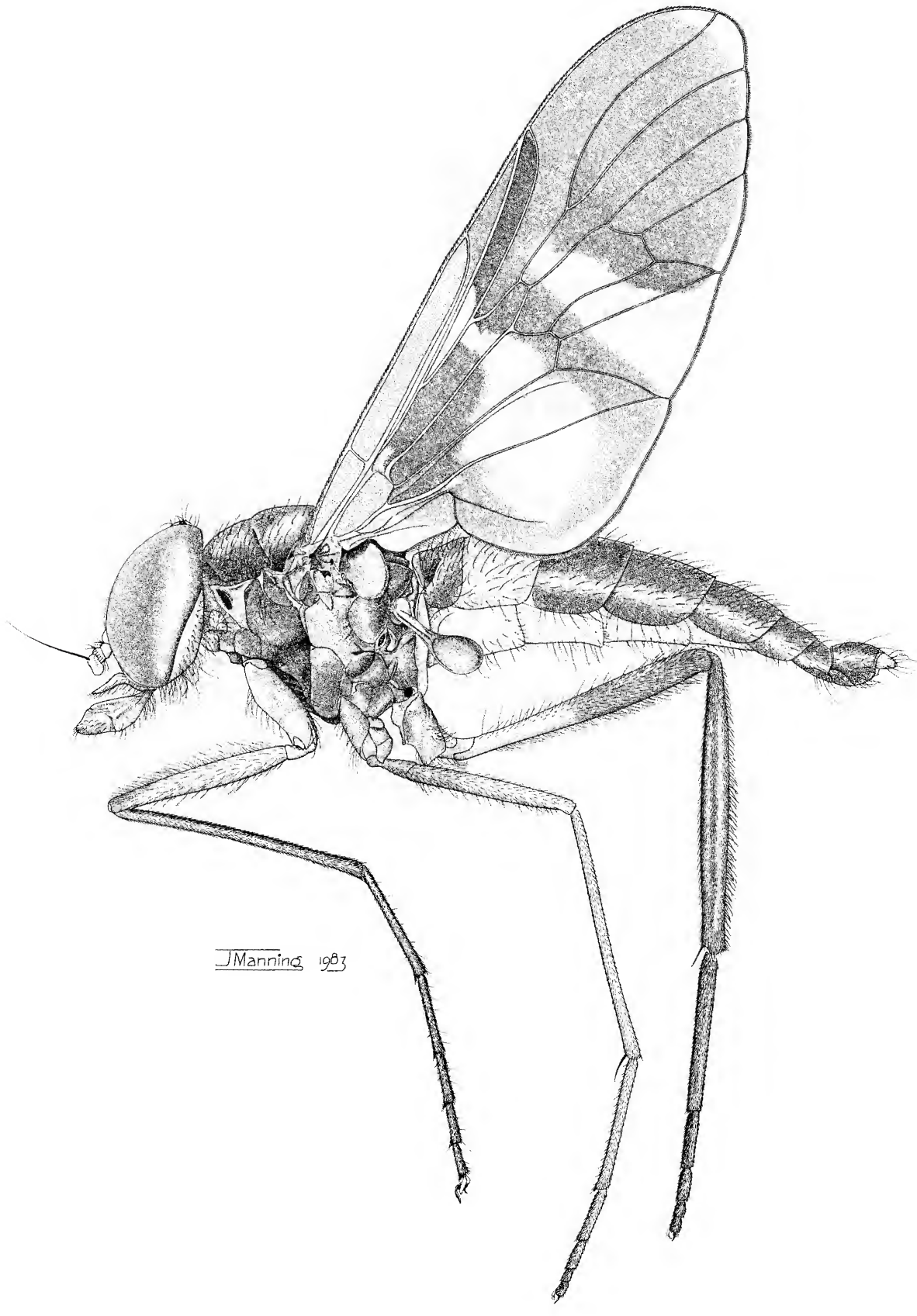
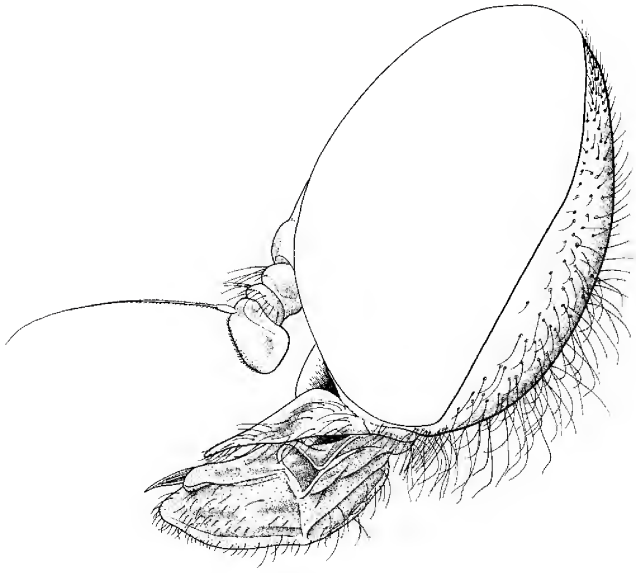
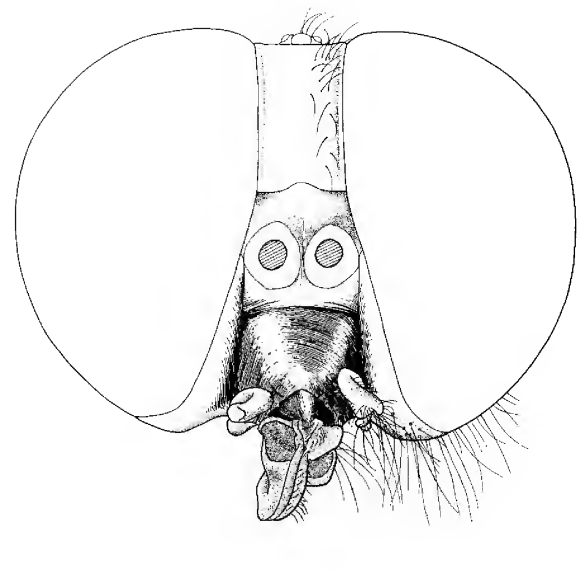


Figure 1. *Suraginella macalpinei* n.gen., n.sp. Male.



Figures 2. *Suraginella macalpinei* n.gen., n.sp. Female head in lateral view.



Figures 3. *Suraginella macalpinei* n.gen., n.sp. Female head in frontal view.

Relationships

The comparison made above of *Suraginella* and *Suragina* makes it clear that the general similarity between them is illusory, and probably these genera are not closely related. Parts of the resemblance—notably the head form, robust proboscis, curved palpi, enlarged postpedicel, and elongate legs—are almost certainly associated with haematophagy and thus could be convergent (the probability that *Suraginella macalpinei* is a bloodsucker is discussed below). Several features of *Suraginella* appear to be apomorphies and warrant examination:

- Form of the gonostyle: the large basal extension (Fig. 5) is unique and an autapomorphy; other athericids have a simple, finger-shaped gonostyle.
- Cell m_3 closed, stalked in some specimens (as in Fig. 1). In the athericine *Xeritha plaumanni* Stuckenberg, 1966 of Brazil, this cell is closed and long-stalked. The only other athericid I know to have m_3 completely closed is an undescribed Peruvian species of "*Suragina*" (the generic status of the neotropical *Suragina*-like athericids requires reassessment). The condition is incipient in various Old World *Suragina* species that have m_3 narrowed apically.
- Small, regularly spaced, erect setae are present dorsally in the female on much of R_{4+5}, the basal third approximately of R_5, and along the entire length of CuA (absent on CuA_1 and CuA_2). This sexual dimorphism is notable; it occurs also in the type series of *Xeritha plaumanni*.

Thus, on two counts—closed m_3, and dorsal setation of certain veins in the female—*Suraginella* and *Xeritha* share apomorphies, and a close relationship between them deserves consideration.

Xeritha plaumanni was described from Nova Teutonia in the southern Santa Catarina Province (27°11'S 52°23'W). I have since seen a series, now in the Natal Museum, with the following label data: [Brazil] Alto Itatiaia / Alt. 2000m / Rio Janeiro [approximately 22°30'S 44°37'W]. This new record shows that the species occurs widely in the old coastal highlands of SE Brazil. Apart from the original description, the only other reference to this genus is by Sinclair *et al.* (1993); they note that the gonocoxal apodemes, which are apomorphically elongate in Athericidae and Tabanidae, were illustrated by me as being very short in *X. plaumanni* (Stuckenberg, 1966, fig. 7). I have confirmed that they are short in a new dissection. Another autapomorphy, not previously noted though I inadvertently showed it in the drawing, is that the endoaedeagal process (a term coined by Sinclair *et al.* for a sclerotised, pointed lobe projecting posteriorly from the end of the ejaculatory apodeme into the sperm sac) in *X. plaumanni* is in the form of a long slender rod, almost equal in length to the ejaculatory apodeme. In other athericids, as stated by Sinclair *et al.*, this process is reduced to a very short subtriangular point. The elongate form in *X. plaumanni* is thus secondary. These two hypopygial features set *Xeritha* apart from all other genera.

Although the condition of closed cell m_3 is rare in Athericidae, it is probably unreliable for cladistic purposes as it would be a simple extension of a trend seen in several genera towards apical narrowing of that cell. The condition is also sporadic and rare in the sister-group Tabanidae, and clearly a consequence of homoplasy in isolated clades. In *Xeritha*, m_3 is additionally distinctive in having a long stalk, suggesting the possibility of an independent development.

The setation of wing veins has not been examined in Athericinae before, although Malloch (1932), followed by Coscarón & Coscarón (1995), used the occurrence of these setae for defining subgenera in *Dasyomma*. The most complete setation occurs in *Dasyomma* s.str.; setae are present (in both sexes) on R_{4+5}, R_5, CuA, CuA_1 and CuA_2. In the other subgenera, the setae are variably absent on CuA and its branches, and on R_5. A survey of Athericinae produced the following results:

A—setation present

- *Succinatherix* Stuckenberg, 1974 (two fossil species, males unknown, in Baltic amber): setae present on R_{4+5}, basal part of R_5, and CuA, in *Succinatherix setifera* Stuckenberg; absent in *S. avita* Stuckenberg.
- *Atherix* Meigen, 1803, s.str. [species similar to *A. ibis* (Fabricius, 1798)]: setation usually sexually dimorphic, variable within and between species: present on R_{4+5} in ♀ *A. basilica* Nagatomi, 1958, ♀ *A. ibis ibis* (some populations), ♀ *A. ibis japonica* Nagatomi, 1958, ♂ *A. pachypus* Bigot, 1887, ♀ *A. lantha* Webb, 1977, ♀ *A. variegata* Walker, 1848; present on CuA in ♂ ♀ *A. ibis ibis* (variable, sometimes absent), ♂ ♀ *A. ibis japonica*, ♂ *A. pachypus*, ♀ *A. basilica*. The most complete setation was found in *A. ibis japonica*: ♂ entire CuA; ♀ R_{4+5}, CuA, CuA_2 basally.
- *Atrichops* Verrall, 1909: setae absent on CuA in both sexes; ♂ has setae on R_{4+5}, usually extending onto basal part of R_5; in ♀ present on R_{4+5} and extending variably onto R_5 (from short basal section to entire vein, differing between species).
- *Xeritha* Stuckenberg: type series, ♂ setae absent, ♀ on CuA, R_{4+5} except short basal section; Alto Itatiaia series, ♂ setae absent, ♀ setae absent on CuA, present on basal half of R_{4+5}.
- *Suraginella* n.gen.: ♂ setae absent; ♀ on CuA, R_{4+5} except short basal section, R_5 over about basal third.

B—setation absent

- *Suragina* Walker; *Asuragina* Yang & Nagatomi, 1992, *Ibisia* Rondani, 1856, *Pachybates* Bezzi, 1926, *Trichacantha* Stuckenberg, 1955; several undescribed South African genera. All are in the Old World.
- "*Suragina*" species of northern Neotropical and southern Nearctic Regions.

There is no discernible way to polarise the character states of vein setation for cladistic analysis. It is unclear whether the most complete complement of setose veins was acquired as a single development, or if it was acquired progressively, the setae perhaps appearing first on R_{4+5} and later on CuA and its branches. Outgroup comparison with Tabanidae proved uninformative; there is no mention of such setose veins or use of them for taxonomic purposes, in modern faunistic monographs on Tabanidae worldwide. Dr Sixto Coscarón (in litt., 1999) informed me that in neotropical tabanids he has seen them only in some species in the primitive genera *Scaptia* Walker, 1850, *Mycteromyia* Philippi, 1865, and *Fidena* Walker, 1850. An examination of drawings of nearctic tabanid wings in Pechuman & Teskey (1981) revealed that *Pilimas californicus* (Bigot) (fig. 31.31) has setae basally on CuA, and *Diachlorus ferrugatus* (Fabricius) (fig. 31.38) has setae on CuA, CuA_2, and R_{4+5} basad of r-m. No reference to these conditions was made by the authors.

This limited evidence indicates that these setae evolved sporadically and independently in a minority of lineages of Athericidae and Tabanidae, and are of unknown phylogenetic significance. Those athericid genera listed above that have setose veins are a polyphyletic medley. The Baltic amber fossil *Succinatherix setifera* reveals that setose veins were appearing in Athericidae as far back as the Eocene. No sister-group of *Suraginella* can be identified at present.

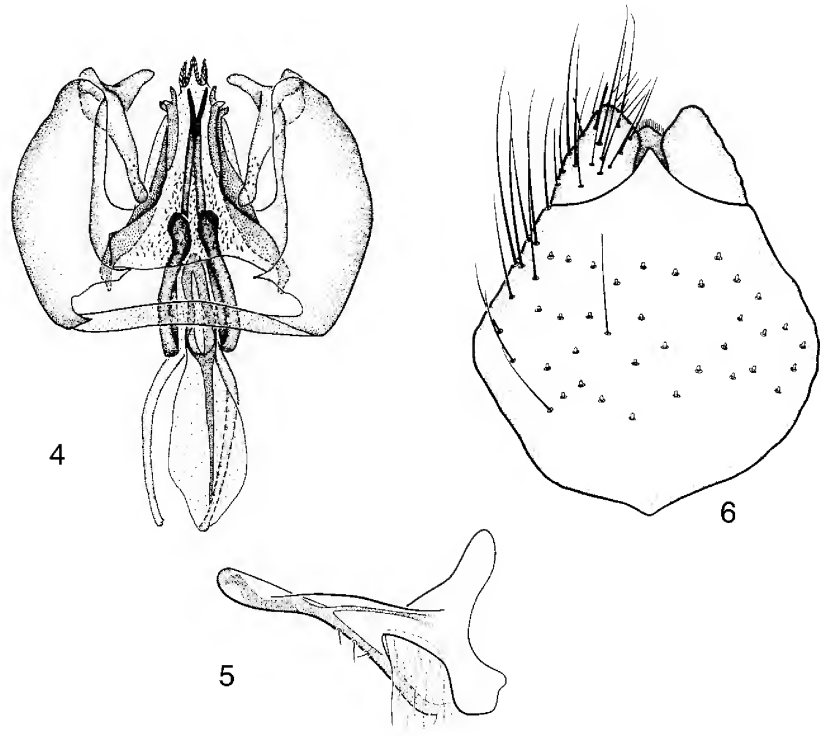
Suraginella—a bloodsucker?

Several records exist of haematophagy by Athericidae; these have been mentioned in most reviews of the bloodsucking habit in Diptera (e.g., Downes, 1958). The following summary extends that by Nagatomi (1962):

- *Suragina longipes* (Bellardi): Man and horses in Mexico.
- *Suragina satsumana* (Matsumura): Cattle in Japan.
- *Suragina bivittata* (Bezzi): Giant Eagle Owl (*Bubo lacteus* Temminck) in South Africa (Stuckenberg & Young, 1973).
- *Atrichops crassipes* (Meigen): Frog (*Rana esculenta* L.) in Europe.
- *Atrichops fontinalis* (Nagatomi) and *A. morimotoi* (Nagatomi): Frogs (*Rana rugosa* Schleger and *R. nigromaculata* Hallowell) in Japan.
- *Dasyomma coeruleum* Macquart and *D. humerale* Malloch: Cattle in Chile (F.W. Edwards, in Malloch, 1932: 200).

During fieldwork in Southern Africa, I have sometimes collected females of *Suragina monogramma* (Bezzi, 1926) with conspicuously red gut contents in the abdomen. Soon after the death of such specimens, the gut contents became blackish and formed a compact mass in the abdomen. It is highly probable that these flies had taken bloodmeals shortly before they were caught. I also observed such dark masses in the abdomen of museum specimens of various other Old World species of *Suragina*; it seems likely, in view of their well-developed mandibulate mouthparts, that the females of all species in this genus are bloodsuckers on vertebrate hosts. Nagatomi (1962) recorded his observations of the two Japanese species of *Atrichops* feeding on frogs; he noted that the gut contents of the flies were reddish immediately after the conclusion of feeding and changed to blackish. Nagatomi found also that oocyte development in these *Atrichops* species was inversely correlated with decrease in the volume of blood in the gut as digestion proceeded. Haematophagy thus appeared to be obligate in this genus.

Of the 12 females available of *S. macalpinei*, six have a dark mass in the abdomen. A test for the presence of blood was attempted by crushing the abdomen of one of them in normal saline solution; the mass was surprisingly hard and shattered into pieces of different sizes. Although the fly had been collected years before, the solution quickly acquired a brownish tinge. A drop was applied to the Blood section of a "Reagent Strip for Urinalysis" ("Multistix 9"—a proprietary product of the Bayer Company); this produced a weak positive reaction. One of the larger pieces, when well soaked in saline, was then placed directly on the strip; within 60 seconds it had produced a much stronger reaction rated "Moderate ++" on the colour scale provided with the strip. This suggests that the fly might have taken a bloodmeal from a vertebrate shortly before its death; however, such a crude test may give false positive results for a variety of reasons. Perhaps a dipterist visiting Cape York Peninsula can catch a



Figures 4–6. *Suraginella macalpinei* n.gen., n.sp. Male genitalia: 4—hypopygium in ventral view; 5—left gonostyle, ventral view; 6—epandrium, dorsal view.

specimen with reddish abdomen and immediately make a smear of the gut contents on a microscope slide. If erythrocytes are present, vertebrate blood will be confirmed; if they are nucleated, the host will have been a bird, frog or reptile.

Biogeography

The distribution of athericids in general is determined by the requirements of the larvae which are rheophilic inhabitants of the beds of streams and rivers, where they prey on small invertebrates, each athericid species occupying a particular section of the river profile. The flies have substrate preferences; autogenous species usually rest on rock surfaces or low vegetation close to or bounded by the water flow, particularly in headwater zones, where they are relatively sedentary. Haematophagous species fly more actively and spread into riparian vegetation, probably impelled by the need to find hosts for bloodmeals; they tend to congregate on particular bushes, shrubbery or small trees, and may range further down river systems, some species of *Suragina* even occurring in riverine woodland along mature, slow-flowing rivers.

Present information is that *Suraginella* is known only from the far north of Cape York Peninsula, in the Iron Range/ Claudie River system, and in the Jardine River system, but future collecting may extend this range. Information is lacking on the preferred habitat and section of river profile the species occupies. Collecting dates for the flies cover a wide period (September to May), which suggests permanence of water in the rivers they occupy.

Accounts of insect biogeography in Cape York Peninsula have focused on rainforest faunas. The extensive review by Kikkawa *et al.* (1981) describes how rainforests occur in three latitudinal zones for which the terms "base-of-peninsula", "mid-peninsula" and "tip-of-peninsula" are established. It appears that *Suraginella* occurs in both "tip-of-peninsula" and "mid-peninsula" zones, but this may be misleading. The nature of riparian vegetation may have little relevance to athericid distribution; the flies are possibly indifferent to the presence of forest, although there may be some significance in the distribution of any vertebrates preferred for bloodmeals, should these be bound to the forest biome. Areas of sclerophyll habitats between the three rainforest regions are thus not necessarily a barrier to *Suraginella*, if they are traversed by rivers that flow regularly.

The faunal component to which *Suraginella* belongs is of interest. Its presence at Iron Range ("mid-peninsula") and the Jardine River system ("tip-of-peninsula"), where many invasive New Guinea faunal elements have become established, raises the possibility that the genus occurs in New Guinea. Kikkawa *et al.* (1981), however, note that some freshwater components of the ancient "Gondwanic" element in Australia, today most diverse in the south, do occur in Iron Range and even in the tip of the peninsula. These are species of Gripopterygidae (Plecoptera) and *Archichauliodes* (Corydalidae: Megaloptera).

Dasyomma is clearly part of the Gondwanic element; its northernmost record is of an undescribed species in the "base-of-peninsula" Atherton Tableland (Paramonov, 1962: 153). If close affinities between *Suraginella* and *Xeritha*

had been found, *Suraginella* probably would be a member of the Gondwanic element. For the present, *Suraginella* is assumed to be another component of the extensive "Autochthonous" fauna of Australia, which developed in isolation from old ancestral stocks throughout the Tertiary (Kikkawa *et al.*, 1981). The distinction between "Gondwanic" and "Autochthonous" in Athericidae thus appears to be at the subfamily level. This is also the case in the palaeogenic dipterous family Blephariceridae; in my view (contrary to Zwick, 1977) its subfamily Edwardsininae is certainly Gondwanic. Perhaps there is biogeographical equivalence between *Suraginella macalpinei* and the blepharicerid *Theischingeria rieki* Zwick, 1998 which is highly distinctive, has no discernible relationships with any other Australasian Blepharicerinae, and is confined to "... only two streams flowing from the highest mountain in one of the largest areas of undisturbed rainforest remaining in Queensland" (the "base-of-peninsula" Mt Bartle Frere).

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Revision of the Genus *Apterodromia* (Diptera: Empidoidea), With a Redefinition of the Tribe Ocydromiini

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ABSTRACT. The Australian endemic genus *Apterodromia* Oldroyd (Diptera: Empidoidea) is revised and includes four apterous species (*A. evansi* Oldroyd, *A. minuta* n.sp, *A. setosa* n.sp., and *A. tasmanica* n.sp.) and eight fully winged species (*A. aurea* n.sp., *A. bickeli* n.sp., *A. irrorata* n.sp., *A. monticola* n.sp., *A. pala* n.sp., *A. spilota* n.sp., *A. tonnoiri* n.sp., and *A. vespertina* n.sp.). The male of *A. evansi* is described and zoogeographic patterns of the genus are discussed. On the basis of wing venation and male terminalia *Apterodromia* is transferred from the Tachydromiinae to the tribe Ocydromiini (subfamily Ocydromiinae). The Ocydromiini is redefined, two new genera (*Neotrichina* n.gen. and *Leptodromia* n.gen.) are described, and all included genera are listed. Keys to major lineages of Australian Empidoidea and Southern Hemisphere genera of Ocydromiini are provided. The following new combinations are listed: *Hoplopeza tachydromiaeformis* (Bezzi), *Leptodromia bimaculata* (Bezzi), *Neotrichina abdominalis* (Collin), *N. digna* (Collin), *N. digressa* (Collin), *N. distincta* (Collin), *N. elegans* (Bigot), *N. fida* (Collin), *N. indiga* (Collin), *N. insignis* (Collin), *N. insons* (Collin), *N. laeta* (Collin), *N. media* (Collin), and *N. obscurata* (Collin).

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The genus *Apterodromia* Oldroyd (Diptera: Empidoidea) was originally described on the basis of a single apterous female from Tasmania (Oldroyd, 1949, fig. 1). Although superficially resembling hemerodromiines, it has been considered to belong to the Tachydromiinae, possibly related to *Tachydromia* Meigen (= *Tachista* Loew) (Oldroyd, 1949; Smith, 1989). Oldroyd (1949) was initially hesitant to describe a new genus on the basis of an apterous specimen, but it has proven to be a unique taxon, distinct from all other Australian empidoids. With greater emphasis on various mass-trapping collecting methods, further species and specimens of this genus have recently been collected for a total of 12 included species. In addition, this new material, including discovery of both males and fully winged species, now allows for a reevaluation of the phylogenetic placement of *Apterodromia* within the Empidoidea.

Materials and methods

This study is based on more than 200 adult specimens of *Apterodromia* housed in the following institutions: American Museum of Natural History, New York (AMNH); Australian National Insect Collection, Canberra (ANIC); Australian Museum, Sydney (AMS); The Natural History Museum, London (BMNH); Canadian National Collection of Insects, Ottawa (CNC); Museum Victoria, Melbourne (MVM); University of Queensland Insect Collection, Brisbane (UQIC); Western Australian Museum, Perth (WAM).

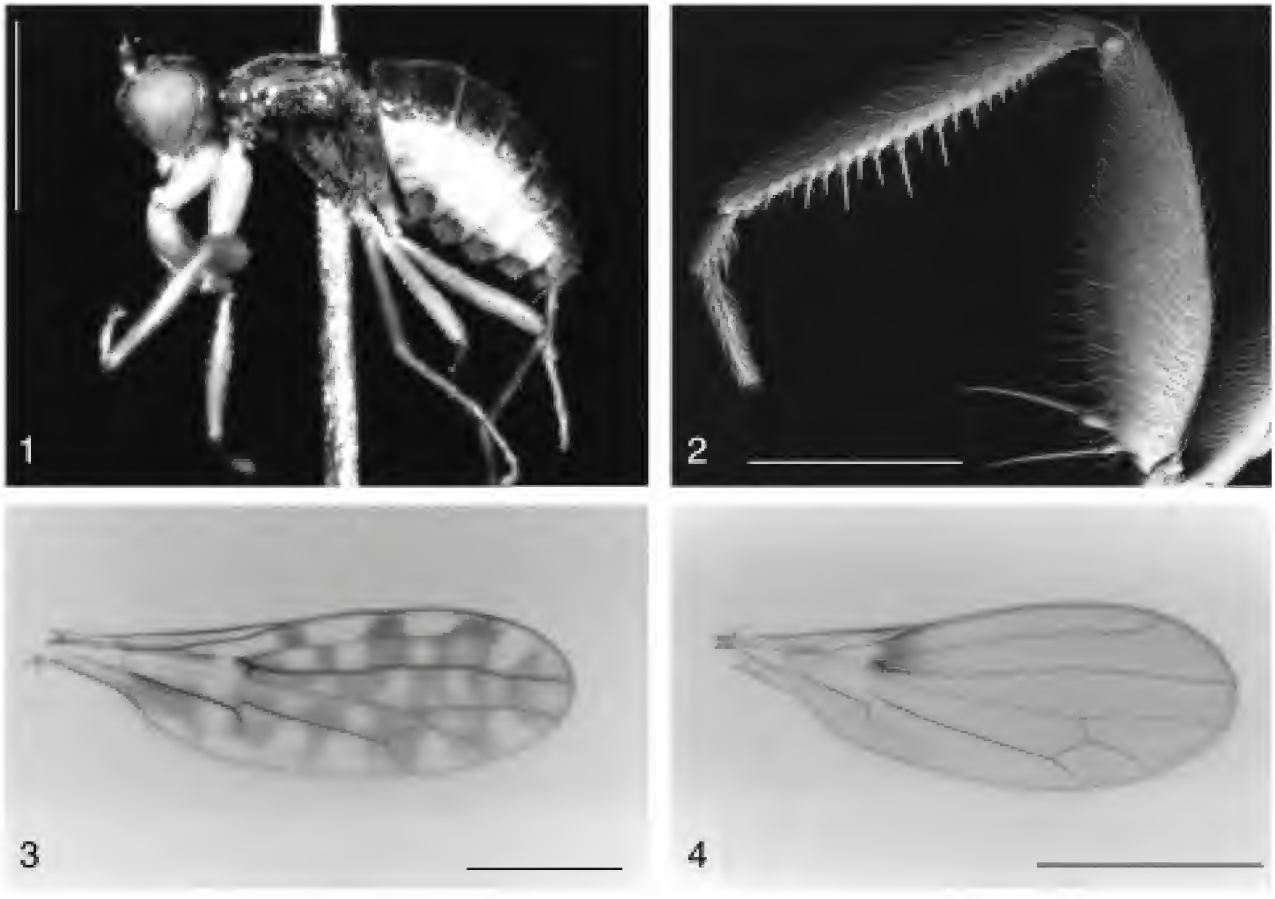
Terms used for adult structures primarily follow those of J.F. McAlpine (1981). Homologies of the male terminalia follow those of Cumming *et al.* (1995) and Sinclair (1996). To facilitate observation, terminalia were macerated in hot 85% lactic acid and immersed in glycerin. Label data of holotypes are cited in full, with original spelling, punctuation and date; lines are delimited by a slash (/), and a semicolon separates data quoted from different labels. In descriptions and key, right and left side of the male terminalia are based on the unrotated position viewed posteriorly, such that in the illustrations the right surstylus appears on the readers left side and vise versa. All male terminalia are figured in their unrotated position, except Fig. 14.

A number of specimens were collected through the use of shallow yellow plastic pans. The use of coloured pans has proven to be an effective and simple method for sampling Dolichopodidae and other empidoids (Pollet & Grootaert, 1987; Bickel, 1994). Pans containing a mixture of water, salt and several drops of detergent were distributed on the forest litter, usually near wet depressions, streams and marshy regions. Specimens of this genus are rarely collected with sweep nets and have only recently been obtained in numbers through the use of mass-trapping methods such as coloured pans and malaise traps. Many apterous species were extracted from wet leaf litter using berlese funnels.

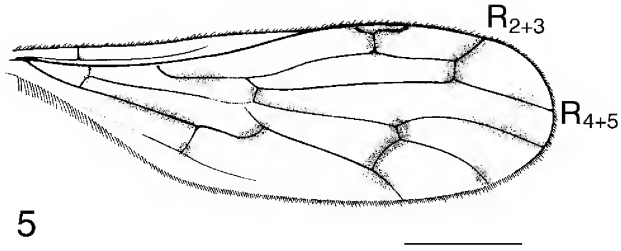
Apterodromia Oldroyd

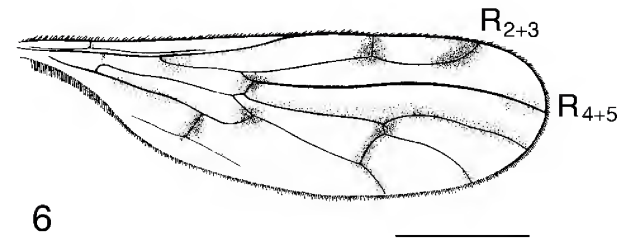
Apterodromia Oldroyd, 1949: 278. Type-species *A. evansi* Oldroyd (original designation).

Diagnosis. Distinguished from other empidoids by the following combination of characters: eyes meet below antennae, with dense ommatrichia; face flattened and angled posteriorly; base of fore femur armed with pair of long spine-like setae, mounted on short tubercles; fore tibia and



Figures 1–4. 1, Female of *Apterodromia evansi*. 2, Scanning Electron Micrograph, left foreleg of *A. irrorata*, posterior view. 3–4, Wing: 3, *A. irrorata*; 4, *A. bickeli*. Scale bars = 1.0 mm, except Fig. 2 where scale bar = 0.5 mm.





Figures 5–6. Wings of *Apterodromia*. 5, *A. spilota*; 6, *A. tonnoiri*. Scale bars = 1.0 mm.

first tarsomere with row of stout ventral setae; fore tibial gland present; proepisternum with 1–2 spine-like seta(e) above fore coxa; three veins emitted from cell dm, A_1 faint below cell cu*p*.

Description. Body length 1.5–4.5 mm.

Male. *Head* black. Eye contiguous on strongly flattened face; facets enlarged below antennae; ommatrichia present, longer on lower facets. Gena not extended below eye; ventral surface of head, posterior to mouth opening clothed in long, pale setulae. Frons broadly linear with sides nearly parallel in winged forms; broadly divergent in apterous forms; entirely clothed in pruinescence. Two pairs of fine ocellar setulae, directed forward. One pair of vertical and 1–2 pairs of upper occipital setae. Antennae inserted above middle of head; scape small, devoid of setulae; pedicel globose; first flagellomere pointed ovate to conical, with long, two-articled apical arista. Palpus tapered to point, two-thirds length of proboscis; palpifer bearing pair of setae; labrum and hypopharynx strongly arched posteriorly; 4 pairs of pseudotracheae present (Fig. 7).

Thorax yellow to entirely black. Thoracic macrotrichia mostly slender and short; acrostichal setulae biserial; dorsocentral setulae uniserial, increasing in length posteriorly; supra-alar setulae biserial; 1 notopleural seta, with scattered setulae; 1 pair of long, apical scutellar setae. Mesonotum entirely pruinescent. Postpronotal lobe differentiated. Prosternum fused to proepisternum forming precoxal bridge; antepronotum well developed, forming wide "neck"-like extension; proepisternum with 1–2 spine-like setae above fore coxa. Meso- and metapleuron clothed entirely in dense whitish pruinescence.

Wings present or absent (reduced to traces of tegula); narrow and blunt-tipped; microtrichia of equal length; costal setae short; basal costal seta short or absent; C ending at M_1; Sc evanescent, fading away beyond Rs; stigma lacking; Rs long arising near base of cell bm; A_1 along lower margin of cell cu*p* faded. Halter (if present) with white knob.

Legs yellow to brown. Fore coxa long, nearly 3 times as long as other coxae; clothed in long, white pile. Fore femur strongly swollen; base armed with pair of long spine-like setae, mounted on short tubercles (Fig. 2); long white pile beneath. Fore tibia somewhat dilated, with posteroventral row of 9–20 spine-like setae, alternating long and short; conspicuous tubular gland near base. First tarsomere of foreleg shorter than second, with posteroventral row of 4 spine-like setae, ending in long projecting spine (Fig. 2); remaining tarsomeres slender, unarmed; mid and hindlegs slender, simple; hind femur thickened apically and bow-legged (apterous species) or straight (winged species).

Abdomen. Sclerites heavily sclerotized in wingless species (except sternites 1 and 2), more thinly sclerotized and usually reduced in size in winged species. Sclerites of segment 8 fused to form wide ring. Hypopygium asymmetrical, rotated approximately 90° to right (Fig. 14). Hypandrium narrow, posterior apex bluntly rounded; dorsal bridge heavily sclerotized; postgonites and ventral apodeme lacking. Epandrium deeply cleft; left surstylus elongate, cylindrical, bearing stout, inner dorsal setae; right surstylus shorter than left, bent nearly perpendicularly to epandrium. Right bacilliform sclerite elongate, bearing stout setae. Cercus usually short, thinly sclerotized, unmodified. Phallus with flexible, lateral cap lined with membrane; ejaculatory apodeme fused to base of phallus.

Female. Similar to male except as follows: winged species with abdomen lightly pigmented, sclerites thinly sclerotized except eighth segment; tergite 8 fused anteroventrally with sternite 8 (Figs. 8–10). Wingless species with all sclerites concolorous with thorax, heavily sclerotized. Cercus long, cylindrical, bearing long, fine setulae. Tergite 10 membranous, sternite 10 triangular. Spermatheca unpigmented, in form of long, slender, trachea-like tube, tightly coiled apically (Fig. 10).

Distribution. This genus is endemic to Australia, where it is widely disjunct, known from northern Queensland (above 700m), Western Australia, and Tasmania (Fig. 32). Despite extensive efforts using various collecting methods (e.g., malaise and yellow pan traps, sweeping) no specimens of *Apterodromia* have been found in New South Wales, Victoria, or ACT (Australian Capital Territory), which are probably the most extensively surveyed regions of Australia. This genus is most diverse in Tasmania, where all four apterous species and two winged species occur.

Biology. The genus has been collected in various humid habitats, including southern temperate and tropical rainforests, wet sclerophyll forests, and alpine herb fields. The adults are presumably predacious on small arthropods inhabiting leaf litter.

Several pairs of species (e.g., *A. aurea* and *A. bickeli*; *A. monticola* and *A. bickeli*; *A. monticola* and *A. pala*) are completely sympatric in Northern Queensland, collected on the same day in a series of malaise or yellow pan traps.

Key to the species of *Apterodromia*

1 Wings and halteres absent 2

—— Wings and halteres present 5

2 Fore femur yellow to yellowish-brown and concolorous with fore coxa, not distinctly darker on basal half; first flagellomere and arista brown, only slightly darker than scape and pedicel ..... *A. tasmanica*

—— Fore femur brown to reddish-brown and darker than fore coxa, distinctly darker on basal half; first flagellomere and arista brownish-black, distinctly darker than scape and pedicel 3

3 Male hypopygium with right surstylus short and blunt, subequal in length to right cercus (Fig. 17); scape and pedicel bright yellow ..... *A. evansi*

—— Male hypopygium with right surstylus longer, at least twice length of right cercus (Figs. 22, 25); scape and pedicel yellowish-brown 4

4 Male hypopygium with right bacilliform sclerite and each surstylus bearing long slender setae (Fig. 25), right surstylus with blunt conical tip; fore tibia reddish-brown, concolorous with basal half of fore femur ..... *A. setosa*

—— Male hypopygium with right bacilliform sclerite and each surstylus bearing short stouter setae (Fig. 22), right surstylus abruptly constricted with narrow tip; fore tibia yellowish-brown, distinctly paler than basal half of fore femur ..... *A. minuta*

5 Wing with clouding along crossveins (Figs. 5, 6) or with irrorations (pale spots) (Fig. 3) 6

—— Wing lacking clouding along crossveins or irrorations (Fig. 4) 9

6 Wing with irrorations (numerous pale spots) (Fig. 3); fore femur lacking row of ventral spine-like setae (as in Fig. 2) 7

—— Wing with clouding along crossveins, lacking irrorations (Figs. 5,6); fore femur with row of ventral spine-like setae 8

7 Proepisternum with one spine-like seta above each fore coxa ..... *A. irrorata*

—— Proepisternum with two spine-like setae above each fore coxa ..... *A. vespertina*

8 Wing with auxiliary crossvein between R_{2+3} and R_{4+5} (Fig. 5); fore coxa with inner row of short stout setae ..... *A. spilota*

—— Wing lacking auxiliary crossvein between R_{2+3} and R_{4+5} (Fig. 6); fore coxa without inner row of short stout setae ..... *A. tonnoiri*

9 Scutum pale, mostly yellow or orange 10

—— Scutum dark, mostly brown or black 11

10 Mesopleuron, metapleuron and mediotergite yellow or yellowish-orange ..... *A. pala*

—— At least lower half of mesopleuron, most of metapleuron and mediotergite black or dark brown ..... *A. aurea*

11 Right bacilliform sclerite of male hypopygium with blunt spine-like setae on basal half (Fig. 23); tergite 8 of female weakly sclerotized on lateral margin subapically, with Y-shaped, dorsoapical sclerite; scutum brownish-orange to brown laterally, paler than anteromedial portion ..... *A. monticola*

—— Right bacilliform sclerite of male hypopygium with blunt spine-like setae along entire length (Fig. 14); tergite 8 of female weakly sclerotized apically, with pair of rectangular dorsomedian sclerites; scutum brown to black laterally, concolorous with anteromedial portion ..... *A. bickeli*

Apterodromia aurea n.sp.

Figs. 7–8, 11–13, 33

Material examined. HOLOTYPE ♂, "AUSTRALIA: N[orthern]. Q[ueens]L[and]D: 11km/ up Mt. Lewis Rd. 900m/ 15–16.iv.1994; rainfor./ D.J. Bickel; ex. yellow/ pans nr. creek; Stop 1/ 16°36'[S] 145°17'E"; "HOLOTYPE/ Apterodromia/ aurea/ Sinclair & Cumming [red label]" (AMS). ALLOTYPE ♀, same data as holotype (AMS). PARATYPES: QUEENSLAND: ♀, Devil's Thumb, 12km NW Mossman, 1000 m, 5.ix.1992, I.D. Naumann (ANIC); 8♀♀ 3♂♂, same data as holotype (ANIC, CNC); 4♂♂, 12km up Mt. Lewis Rd., 860 m, 16°30'S 145°17'E, 15–16.iv.1994, D.J. Bickel (AMS); ♂, 25 km up Mt. Lewis Rd., 1000 m, 16°32'S 145°17'E, 16.iv.1994, B.J. Sinclair (CNC); ♀, 25km up Mt. Lewis Rd., 1000 m, 16°32'S 145°17'E, 21.iv.1994, M. Moulds (AMS); ♀, Mt. Lewis at For. Hut, 1020 m, 16°36'S 145°16'E, 16.iv.1994, D.J. Bickel (ANIC); ♀, Mt. Spurgeon, wet scler. for., tree trunks, 16°26'S 145°12'E, 19.iv.1994, D.J. Bickel (AMS); 2♂♂, ♀, Windsor Tableland, montane for., 1260 m, 16°14'01"S 145°00'14"E, 17–18.iv.1994, D.J. Bickel (AMS).

Diagnosis. Distinguished from other winged species of *Apterodromia* by the scutum and upper half of the pleura coloured golden or orange-yellow, and lower half black. The male terminalia are characterized by blunt, spine-like setae on the basal half of the left surstylus and entire length of the right bacilliform sclerite.

Description. Body length 2.5–3.0 mm.

Male. *Head*. Scape, pedicel and first flagellomere brown; first flagellomere conical.

Thorax with dorsum orange except antepronotum and posterior third of notopleuron black; postpronotal lobe outlined in black. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout. Lower half of mesopleuron black, upper half orange, extending to base of halter; laterotergite orange. Metapleuron and mediotergite black.

Wing infuscate, with dark band from tip of R_1 to tip of cell br; basal costal seta short; cell dm elongate, narrow, nearly twice length of basal cells; M_2 and CuA_1 faded prior to wing margin; cell cu*p* longer than cell bm; CuA_2 convex.

Legs yellowish-brown, except mid and hind coxae tinged with black. Fore coxa slender, parallel-sided, lacking inner setae. Anterior basal spine-like seta of fore femur twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 12 spine-like posteroventral setae.

Abdomen. Sclerites thinly sclerotized and reduced in size. Hypandrium with crown of blunt, apical, spine-like setae (Fig. 13). Posterior margin of epandrium irregular. Left surstylus elongate, cylindrical, bearing blunt, inner dorsal spine-like setae on basal half; right surstylus short, pointed, strongly held inwards (Fig. 11). Right bacilliform sclerite elongate, bearing blunt, spine-like setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 11). Phallus with broad lateral, flexible cap (Fig. 12).

Female. Similar to male except setae of foreleg more pronounced; fore tibia with 12–15 spine-like, posteroventral setae. Tergite 8 weakly sclerotized on lateral margin subapically, with Y-shaped, dorsoapical sclerite bearing several pairs of lateral setae (Fig. 8).

Distribution. Confined to high tablelands in the wet tropics region of northern Queensland near Cairns (Fig. 33).

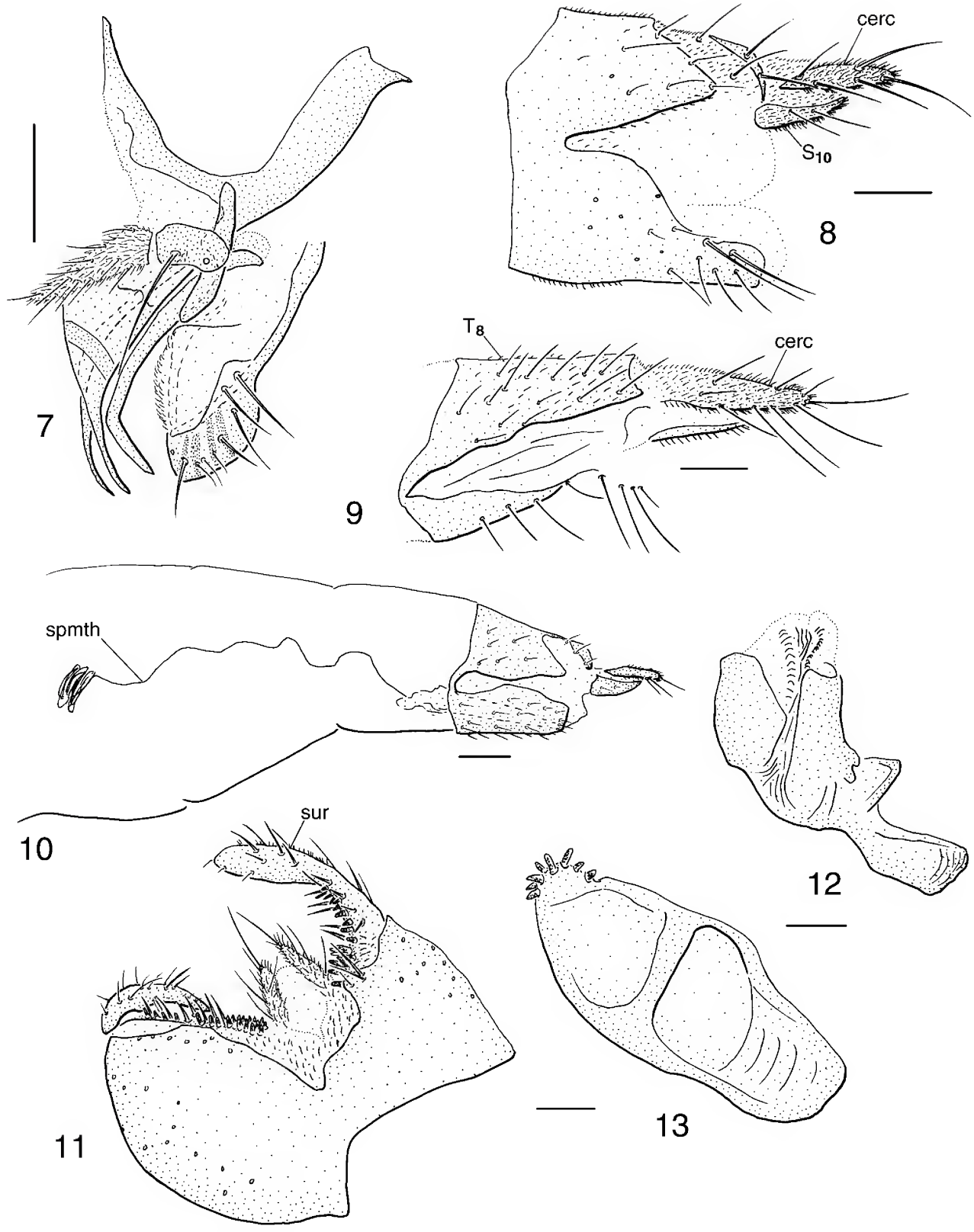
Biology. Collected in cool, submontane rainforests (above 700 m). The vegetation of these forests can be classified into several groupings, including simple microphyll vine-fern forest (MFT). See Adam (1992) for summary of the major rainforest types of northeastern Queensland.

Etymology. The specific name is derived from the Latin *aureus* (golden), referring to the golden or orange coloured thorax of this species.

Apterodromia bickeli n.sp.

Figs. 4, 14–16, 34

Material examined. HOLOTYPE ♂, "AUSTRALIA: N[orthern]. Q[ueens]L[and]D: 11km/ up Mt. Lewis Rd. 900m/ 15–16.iv.1994; rainfor./ D.J. Bickel; ex. yellow/ pans nr. creek; Stop 1/ 16°36'[S] 145°17'E"; "HOLOTYPE/ Apterodromia/ bickeli/ Sinclair & Cumming [red label]" (AMS). ALLOTYPE ♀, same data as holotype (AMS). PARATYPES: QUEENSLAND: 2♂♂, ♀, Bellenden Ker Range, Summit T.V. Sta., 1560 m, rainfor., malaise tp., 17.x–5.xi.1981, Earthwatch/ QLD Museum (ANIC); ♂, Devil's Thumb, 12km NW Mossman, 1000 m, 5.ix.1992, I.D. Naumann (ANIC); 2♂♂, 2♀♀, Hugh Nelson Range, 1150 m, 17°27'S 145°29'E, 1.xii.1994–3.i.1995, 6.iii–4.iv., 1.viii–1.ix.1995, L. Umback, P. Zborowski (ANIC); 10♂♂, 5♀♀, Longlands Gap, 17°28'S 145°29'E, 1150 m, 4.iv–2.v.1995, 1.vi–3.vii., 1.viii–1.xi.1995, 30.xi.1995–3.i.1996, L. Umback, P. Zborowski (ANIC); 3♂♂, 8♀♀, Massey Ck., 17°37'S 145°34'E, 1000 m, 1.xii.1994–6.iii.1995, 5.iv–3.v.1995, P. Zborowski (ANIC); 5♂♂, 17♀♀, Mt. Edith, 17°06'S 145°37'E, 1050 m, 4.ii–6.iv.1995, 4–31.v.,



Figures 7–13. 7, Mouthparts of *Apterodromia aurea*, lateral view. 8–10, Female terminalia, lateral view: 8, *A. aurea*; 9, *A. irrorata*; 10, *A. pala*. 11–13, Male terminalia of *A. aurea*: 11, epandrium and cerci, dorsal view; 12, phallus; 13, hypandrium, dorsal view. Scale bars = 0.1 mm. Abbreviations: cerc, cercus; S_{10}, sternite 10; spmth, spermatheca; sur, surstylus; T_8, tergite 8.

30.v–31.viii.1995, L. Umback, P. Zborowski (ANIC); ♂, 4km up Mt. Edith Rd., Danbulla S.F., 800 m, 22–27.iv.1994, B.J. Sinclair (CNC); ♂, Mt. Edith For., 1.5m off Danbulla Rd. 6.v.1967, D.H. Colless (ANIC); 5♂♂, 2♀♀, Mt. Fisher, 17°33'S 145°32'E, 1150 m, 4.ii–21.iii.1995, 26.iii–2.v., 1–30.viii.1996, malaise tp., P. Zborowski (ANIC); 8♂♂, 16♀♀, Mt. Haig, 17°06'S 145°36'E, 1150 m, 1.xii.1994–3.i.1995, 6.iv–4.v.1995, 4–31.v., 30.vi–29.ix.1995, L. Umback, P. Zborowski (ANIC); ♂, Mt. Hypipamee N.P., 960 m, rainfor., 17°26'S 145°29'E, 13–27.iv.1994, D.J. Bickel (AMS); 2♂♂, 2♀♀, same data as holotype (AMS); ♂, Mt. Lewis Rd. at For. Hut, 1020 m, pans, 16°36'S 145°16'E, rainfor., 16.iv.1994, D.J. Bickel (AMS); ♀, 12km up Mt. Lewis Rd., 860 m, 16°30'S 145°17'E, 15–16.iv.1994, D.J. Bickel (AMS); ♀, 5–8 m Mt. Lewis Rd. off Mossman–Mt. Mulloy Rd., 22.iv.1967, D.H. Colless (ANIC); 2♂♂, ♀, Mt. Windsor Tableland, For. Hut, 1060 m, 16°15'42"S 145°02'25"E, 16–27.iv.1994, D.J. Bickel (AMS); 2♂♂, Windsor Tableland, montane for., 1260 m, 16°14'01"S 145°00'14"E, 17–18.iv.1994, D.J. Bickel (AMS). Several duplicates have been deposited in UQIC, CNC and AMNH.

Diagnosis. Distinguished from other winged species of *Apterodromia* by the mostly black thorax with only small posterior areas brownish. The male terminalia are characterized by blunt, spine-like setae distributed for nearly the length of the left surstylus and entire length of the right bacilliform sclerite. See *A. monticola* for additional distinguishing features.

Description. Body length 2.0–2.8 mm.

Male. *Head.* Scape, pedicel and first flagellomere brown; first flagellomere conical.

Thorax entirely black, except for golden iridescence on margin of scutum at base of wing. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite black.

Wing (Fig. 4) infuscate, with dark band from tip of R_1 to tip of cell br; basal costal seta short; cell dm elongate, narrow, nearly twice length of basal cells; M_2 and CuA_1 faded prior to wing margin; cell cu*p* longer than cell bm; CuA_2 convex.

Legs yellowish-brown, except mid and hind coxae tinged with black. Fore coxa slender, parallel-sided, lacking inner setae. Anterior basal spine-like seta of fore femur less than twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 14–15 spine-like posteroventral setae.

Abdomen. Sclerites thinly sclerotized and reduced in size. Hypandrium with crown of blunt, apical, spine-like setae (Fig. 15). Posterior margin of epandrium with pair of deep U-shaped clefts. Left surstylus elongate, cylindrical, bearing blunt, spine-like setae along most of inner dorsal margin; right surstylus short, pointed, strongly arched. Right bacilliform sclerite elongate, bearing blunt, spine-like setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 14). Phallus with broad lateral, flexible cap (Fig. 16).

Female. Similar to male except setae of foreleg more pronounced. Tergite 8 weakly sclerotized apically, with pair of rectangular dorsomedian sclerites, bearing transverse row of 3 subapical setae.

Distribution. Widespread in the high tablelands (above 700 m), in the wet tropics region of northern Queensland near Cairns (Fig. 34).

Biology. Adults appear to be present year-round, found in the cooler wet rainforests of the tablelands west of Cairns and montane forests of the Bellenden Ker Range. Some of the first specimens collected of this species were from the summit region of Mt. Bellenden Ker (1560 m), one of the highest points in northern Australia. The vegetation type on the summit is simple microphyll vine-fern thicket which represents a true tropical upper montane rainforest (Adam, 1992).

Etymology. The name *bickeli* is proposed in thanks to Dr Daniel J. Bickel (AMS) whose collecting efforts in northern Queensland have markedly increased our knowledge of this rare empidid genus.

Apterodromia evansi Oldroyd

Figs. 1, 17–19, 35

Apterodromia evansi Oldroyd, 1949: 279.

Material examined. HOLOTYPE ♀, "Type [red borded circle]"; "TASMANIA/ J.W. EVANS"; "Apterodromia/ evansi n.sp ♀/ det. H. Oldroyd 1948/ HOLOTYPE" (BMNH).

Additional material. TASMANIA: ♂, ♀, Waldheim, Cradle Mt., 12–14.ii.1967 (UQIC); ♀, Hartz Mtns N.P., Hartz Rd., 740 m, eucalyp. scrub, 8–10.ii.1980 (ANIC).

Diagnosis. Distinguished from other apterous species by the darkly coloured basal half of the fore femur (including tubercles of spine-like setae), bright yellow basal antennal segments and blunt, short right surstylus.

Description. Body length 2.0–2.5 mm.

Male. *Head.* Scape and pedicel bright yellow; first flagellomere and arista dark brown; first flagellomere pointed ovate.

Thorax entirely black (Fig. 1). Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite black.

Wings. Absent. Halter absent.

Legs. Fore coxa pale yellow; lacking inner setae. Fore femur strongly attenuated apically; basal half of posterior surface reddish-brown, including tubercles of basal setae; anterior basal spine-like seta less than twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 9 spine-like posteroventral setae. Fore tibia, first and second tarsomeres reddish-brown, remaining tarsal segments brown. Mid and hind coxae black, except yellowish at apex. Mid and hind femora, tibiae, first tarsomere and basal half of second tarsomere reddish-brown, remaining tarsal segments brown.

Abdomen. Sclerites heavily sclerotized (except sternites 1 and 2 which are weakly sclerotized); tergites 1 and 2 immovably fused together with intersegmental suture still obvious at lateral margin. Hypandrium with scattered, pointed, stout setae near apex (Fig. 19). Posterior margin

of epandrium deeply cleft, rectangular. Left surstylus elongate, cylindrical, bearing long, tapering setae on inner dorsal margin near base; right surstylus short, blunt, geniculate near base, bearing long, stout setae along outer margin. Right bacilliform sclerite elongate, bearing stout setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 17). Phallus with small oval flexible cap, with narrow extension (Fig. 18).

Female. Similar to male except setae of foreleg more pronounced; fore tibia with row of 11 spine-like posteroventral setae. Tergite 8 sclerotized along entire margin, not subdivided apically.

Distribution. Confined to wet forests of western Tasmania (Fig. 35). Oldroyd (1964: 95) erroneously listed this species from New Zealand.

Biology. This species was collected at an altitude of approximately 900 m at Cradle Mtn N.P.

Apterodromia irrorata n.sp.

Figs. 2–3, 9, 20–21, 32

Material examined. HOLOTYPE ♂, "AUST[ralia]:WA [Western Australia] Pemberton/ Crowea St. For./ Nov.–Dec. 1979/ S.J. Curry"; "HOLOTYPE/ Apterodromia/ irrorata/ Sinclair & Cumming [red label]" (ANIC). ALLOTYPE ♀, same data as holotype. PARATYPES: WESTERN AUSTRALIA: ♂, Pemberton, 3.xii.1936, K.R. Norris (ANIC); 21♂♂, 14♀♀, same locality as holotype, xi–xii.1976, 1977, 1979, S.J. Curry (ANIC); 2♀♀, Pemberton, karri for., 30.xi–2.xii.1998, B.J. Sinclair (AMS); ♂, 10km SE Pemberton, karri for., yellow pans, 1–2.xii.1998, B.J. Sinclair (CNC). Several duplicates have been deposited in AMS, CNC, and WAM.

Diagnosis. Distinguished from all other winged species of *Apterodromia* by irrorated pattern on the wings and 1 spine-like proepisternal seta. The male terminalia are characterized by short, pointed setae on basal two-thirds of the left surstylus and entire length of the right bacilliform sclerite.

Description. Body length 2.5–3.0 mm.

Male. *Head*. Scape, pedicel, first flagellomere and arista dark brown; first flagellomere conical to subtriangular.

Thorax dark brown to black. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta slender. Mesopleuron, metapleuron and mediotergite brown to black.

Wing (Fig. 3) infuscate; basal costal seta short, slender; veins weakly undulating; numerous pale spots or irrorations: cell r_1 with 3 broad spots, cell r_{2+3} with 4–5 round spots, cell r_{4+5} with 5 spots, 2–3 spots in cell dm, 2 spots in cell m_1, cell m_2 with 1 large spot, cell cua_1 with 2 spots, cell cu*p* with 1 apical spot. Auxiliary crossveins lacking; cell dm narrow, ca. one-third longer than cell bm; M_2 and CuA_1 faded prior to wing margin; cell cu*p* longer than cell bm; CuA_2 convex.

Legs. Fore coxa usually yellow, sometimes dark brown; lacking inner setae. Fore femur brown on posterior face, tubercles of basal setae yellow; femur not strongly attenuated apically; anterior basal spine-like seta ca. equal in length to posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 14–16 spine-like posteroventral setae (Fig. 2), sometimes with 14–20 spine-like setae. Fore tibia and first tarsomere yellow, remaining tarsal segments dull brown. Mid and hind coxae brown, becoming black basally. Mid and hind femora with basal fourth pale yellow, remaining femora brown, darker towards apex; remaining leg segments yellowish-brown gradually darkening on tarsal segments.

Abdomen. Sclerites lightly sclerotized. Hypandrium with scattered, pointed, stout setae near apex. Posterior margin of epandrium deeply cleft, U-shaped. Left surstylus elongate, cylindrical, outer margin with long setae and pile of setulae; inner dorsal margin near base with dense stout setae. Right surstylus less than half length of left surstylus, geniculate near base, bearing long, stout basal setae; tapered to narrow apex. Right bacilliform sclerite elongate, bearing short, stout setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 20). Phallus with oval flexible cap (Fig. 21).

Female. Similar to male, except spine-like setae more pronounced. Tergite 8 sclerotized along entire margin, not subdivided apically (Fig. 9).

Distribution. This species is confined to the extreme southwestern corner of Australia (Western Australia) (Fig. 32).

Biology. All known specimens of this species were collected in wet sclerophyll forests dominated by giant Karri trees (*Eucalyptus diversicolor*). These forests grow in deep red clay loams and receive more than 750 mm of annual rainfall.

Two female specimens were collected by sweep net while walking a hiking trail. They appeared slow moving in the net, with their forelegs held outstretched in front.

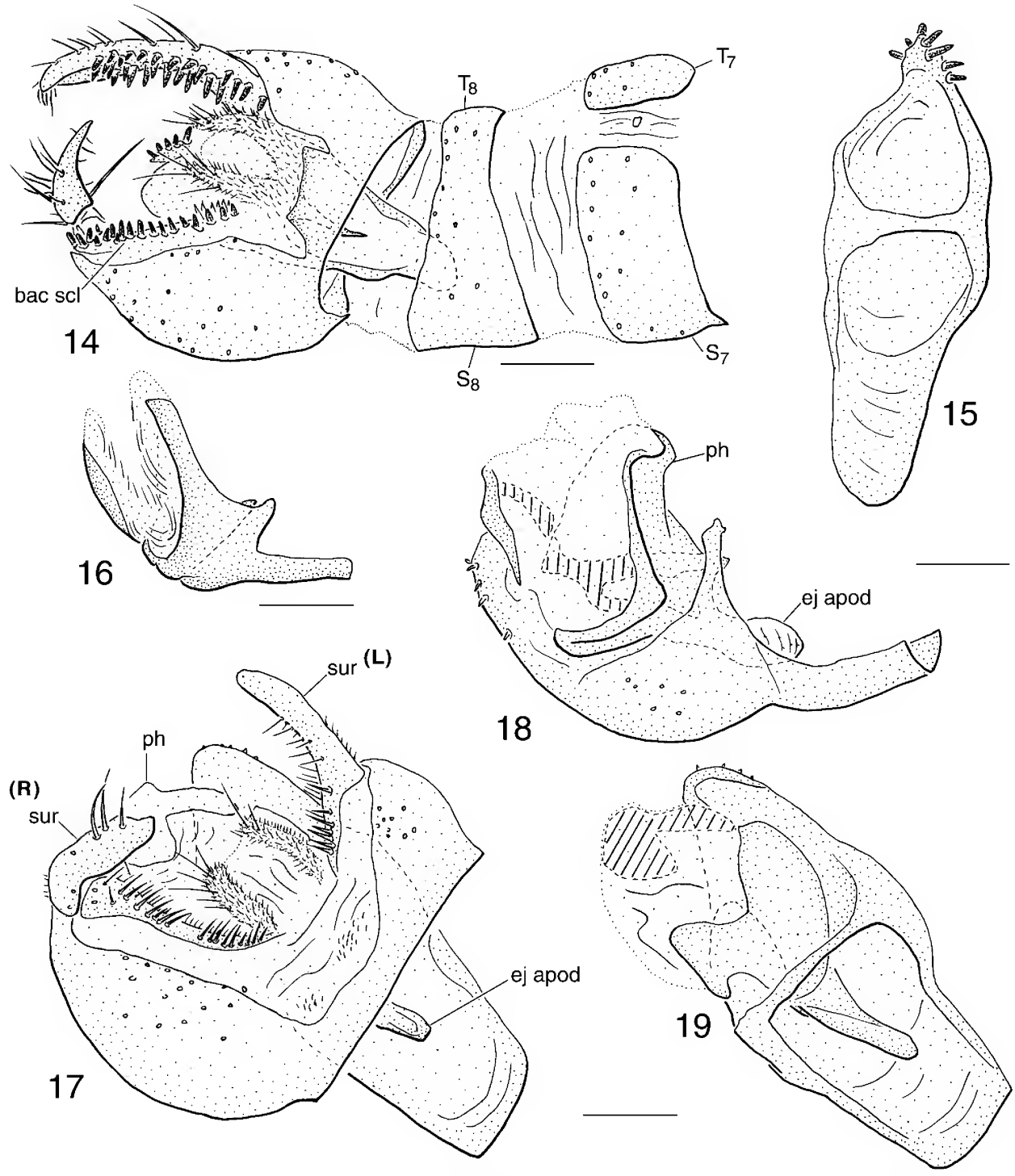
Etymology. The specific name is derived from the Latin *irroratus*, meaning bedewed, in reference to the pale punctations or clear areas on the wings.

Remarks. There is also a dark form with 14–20 posteroventral spine-like setae on the fore tibia and the fore coxa is dark brown. The male terminalia are more darkly pigmented but otherwise identical to the paler form. Both forms are sympatric, collected from Crowea State Forest and are considered a result of intraspecific variation.

Apterodromia minuta n.sp.

Figs. 22, 35

Material examined. HOLOTYPE ♂, "AUSTRALIA: Tasmania/ NW 5km Renison Bell/ 180m, Berlese rainfor-/ est litter, 1lvl[19]87l N.I. Platnick *et al.*"; "HOLOTYPE/ Apterodromia/ minuta/ Sinclair & Cumming [red label] (ANIC). ALLOTYPE ♀, "AUST[ralia]: TAS[mania]: 7 km WNW/ Mt. Field/ 1.ii.1980/ Lawrence & Weir"; "ALLOTYPE/ Apterodromia/ minuta/ Sinclair & Cumming [red label]" (ANIC). PARATYPES: TASMANIA: ♂, same data as allotype (ANIC); ♀, Bubb's Hill [42°07'S 145°46'E], W Victoria Pass, 28.iv.1987, berlese leaf litter, N.I. Platnick *et al.* (CNC); ♀, Mt. Rufus, Lk. St. Clair NP, berlese moss +



Figures 14–19. Male terminalia of *Apterodromia*. 14–16, *A. bickeli*: 14, postabdomen, ventrolateral view; 15, hypandrium, dorsal view; 16, phallus. 17–19, *A. evansi*: 17, terminalia, dorsal view; 18, hypandrium and phallus, lateral view; 19, hypandrium and phallus, dorsal view. Scale bars = 0.1 mm. Abbreviations: bac scl, bacilliform sclerite; ej apod, ejaculatory apodeme; L, left; ph, phallus; R, right; S, sternite; sur, surstylus; T, tergite.

rainfor. litter, 29.iv.1987, N.I. Platnick *et al.* (AMNH); ♀, Mt. Rufus, Lk. St. Clair NP, 29.iv.1987, berlese litter from beech eucalyptus for., N.I. Platnick *et al.* (AMNH); ♀, 0–10 km W Strathgordon, N. Mt. Sprent, 290 m, 27.iv.1989, berlese moss + litter wet rainfor., N.I. Platnick *et al.* (AMNH).

Diagnosis. Distinguished from the other apterous species by its yellowish-brown forelegs, yellowish tubercles at base of fore femur, and long right surstylus with an apical notch.

Description. Body length 1.8–2.0 mm.

Male. *Head*. Scape brown; pedicel yellowish-brown; first flagellomere and arista dark brown; first flagellomere pointed ovate.

Thorax entirely black. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite black.

Wings. Absent. Halter absent.

Legs. Fore coxa pale yellow; lacking inner setae. Fore femur not strongly attenuated apically; basal half of posterior surface with dark brown band, tubercles of basal setae yellow; anterior basal spine-like seta less than twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 9 spine-like posteroventral setae. Fore tibia yellowish-brown, tarsal segments gradually darker apically. Mid and hind coxae yellowish-brown, becoming black basally. Mid and hind femora with broad brown band on basal half, more distinct on hindleg; remaining leg segments yellowish-brown gradually darkening on tarsal segments.

Abdomen. Sclerites heavily sclerotized (except sternites 1 and 2 which are weakly sclerotized); tergites 1 and 2 immovably fused together with intersegmental suture still obvious at lateral margin. Hypandrium with scattered, pointed, stout setae near apex. Posterior margin of epandrium deeply cleft, U-shaped. Left surstylus elongate, cylindrical, sparsely setose apically; inner dorsal margin near base with dense stout setae. Right surstylus nearly as long as left surstylus, geniculate near base, bearing long, stout basal and ventrolateral setae; from posterior view apex sharply constricted forming narrow tip. Right bacilliform sclerite elongate, bearing short stout setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 22). Phallus with small oval flexible cap.

Female. Similar to male except mid and hindlegs yellowish-brown, banding not as distinct. Tergite 8 sclerotized along entire margin, not subdivided apically.

Distribution. This species is known from the wet forests of western Tasmania (Fig. 35).

Biology. This species was collected in leaf litter and moss samples which were first sifted and then extracted using berlese funnels.

Etymology. The specific name is derived from the Latin *minutus*, in reference to the very small size of this species.

Apterodromia monticola n.sp.

Figs. 23, 34

Material examined. HOLOTYPE ♂, "QLD: Mt. Haig, 1150m/ 17.06S 145.36E, P./ Zborowski, F.I.|malaise/ 1-xii-94–3-i-1995"; "HOLOTYPE/ Apterodromia/ monticola/ Sinclair & Cumming [red label]" (ANIC). ALLOTYPE ♀, "QLD: Hugh Nelson Range/ 1150 m, 17.27S 145.29E, P./ Zborowski, F.I.|malaise/ 3-i to 5-ii-1995"; "ALLOTYPE/ Apterodromia/ monticola/ Sinclair & Cumming [red label]" (ANIC). PARATYPE: QUEENSLAND: ♂, Longlands Gap, 17°28'S 145°29'E, 1150 m, 4.iv–2.v.1995, P. Zborowski (AMS).

Diagnosis. Distinguished from other winged species of *Apterodromia*, except *A. bickeli*, by a dark thorax and clear wings. Generally distinguishable from *A. bickeli* by the colouration of the scutum laterally, which is paler than the medial portion. In addition, unlike *A. bickeli*, the right bacilliform sclerite of the male lacks blunt spine-like setae on the apical half, and the female possesses a subdivided Y-shaped dorsoapical sclerite on tergite 8.

Description. Body length 2.0–3.0 mm.

Male. *Head*. Scape, pedicel and first flagellomere brown; first flagellomere conical.

Thorax brown to black, with some golden iridescence on margin of scutum at base of wing; scutum paler laterally, brownish-orange to brown. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite brown to black.

Wing infuscate, with dark band from tip of R_1 to tip of cell br; basal costal seta short; cell dm elongate, narrow, nearly twice length of basal cells; M_2 and CuA_1 faded prior to wing margin; cell cu*p* longer than cell bm; CuA_2 convex.

Legs yellowish-brown, except mid and hind coxae tinged with black. Fore coxa slender, parallel-sided, lacking inner setae. Anterior basal spine-like seta of fore femur less than twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 14–15 spine-like posteroventral setae.

Abdomen. Sclerites thinly sclerotized and reduced in size. Hypandrium with crown of blunt, apical, spine-like setae. Posterior margin of epandrium uneven, sculptured. Left surstylus elongate, cylindrical, bearing blunt, spine-like setae along much of inner dorsal margin; right surstylus short, pointed, strongly arched. Right bacilliform sclerite elongate, bearing blunt, spine-like setae on basal half. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 23). Phallus with broad lateral, flexible cap.

Female. Similar to male except setae of foreleg more pronounced. Tergite 8 weakly sclerotized on lateral margin subapically, with Y-shaped, dorsoapical sclerite bearing several pairs of lateral setae.

Distribution. Confined to high tablelands in the wet tropics region of northern Queensland near Cairns (Fig. 34).

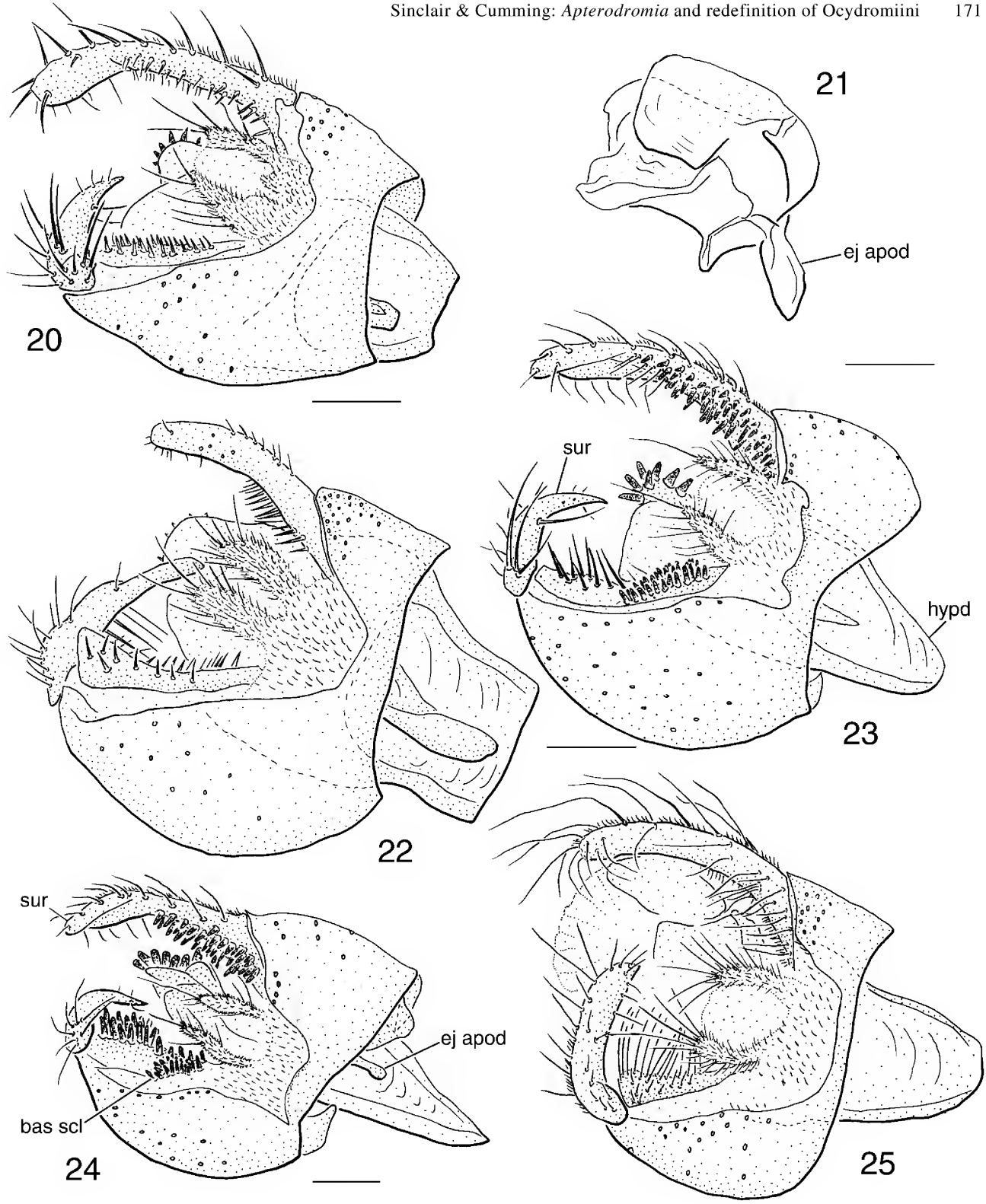
Biology. Collected in cool, submontane rainforests at 1150 m.

Etymology. A noun in aposition, derived from the Latin *monticola* (mountaineer), in reference to the montane habitat where this species is found.

Apterodromia pala n.sp.

Figs. 10, 24, 33

Material examined. HOLOTYPE ♂, "AUST:QLD: Massey Ck./ 4.ii–6.iii.1995/ P. Zborowski, 1000m/ 17°37'S 145°34'E/ ex. malaise trap"; "HOLOTYPE/ Apterodromia/ pala/ Sinclair & Cumming [red label]" (ANIC). ALLOTYPE ♀, "AUST:QLD:Massey Ck./ 5.iv–3.v.1995/ P. Zborowski, 1000m/ 17°37'S 145°34'E"; "ALLOTYPE/ Apterodromia/



Figures 20–25. Male terminalia of *Apterodromia*. 20–21, *A.* irrorata: 20, terminalia, dorsal view; 21, phallus. 22, *A. minuta*, dorsal view. 23, *A. monticola*, dorsal view. 24, *A. pala*, dorsal view. 25, *A. setosa*, dorsal view. Scale bars = 0.1 mm. Abbreviations: bac scl, bacilliform sclerite; ej apod, ejaculatory apodeme; hypd, hypandrium; sur, surstylus.

pala/ Sinclair & Cumming [red label]" (ANIC). PARATYPES: QUEENSLAND: ♂, 2♀♀, Hugh Nelson Range, 1150 m, 17°27'S 145°29'E, 1.xii.1994–3.i.1995, 3.i–5.ii.1995, 4.iv–2.v.1995, F.I. and malaise tps, P. Zborowski (AMS, ANIC); ♀, Longlands Gap, 17°28'S 145°29'E, 1150 m, 1.viii–1.ix.1995, malaise tp., L. Umback (CNC); 3♂♂, 2♀♀, Massey Ck., 17°37'S 145°34'E, 1000 m, 4.ii–6.iii.1995, 3.v–4.vii.1995, 27.ii–26.iii.1996, malaise tp., P. Zborowski (ANIC); ♂, ♀, Mt. Edith, 17°06'S 145°37'E, 1050 m, 17.iii–6.iv.1995, 4–31.v.1995, malaise tp., P. Zborowski (AMS); ♂, Mt. Haig, 17°06'S 145°36'E, 1150 m, 4–31.v.1995, malaise tp., P. Zborowski (CNC);

♀, Mt. Lewis Rd. via Julatten, 1000 m, 10.x–11.xi.1987, rainfor. interc.tp., A. Walford-Huggins (ANIC).

Diagnosis. Distinguished from other winged species of *Apterodromia* by an almost entirely yellow to orange thorax and clear wings. The male terminalia are characterized by blunt, spine-like setae on the basal half of the left surstylus and entire length of the right bacilliform sclerite.

Description. Body length 2.5–3.5 mm.

Male. *Head*. Scape, pedicel and first flagellomere brown; first flagellomere conical.

Thorax almost entirely yellow to orange. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout.

Wing infuscate, with dark band from tip of R_1 to tip of cell br; basal costal seta short; cell dm elongate, narrow, nearly twice length of basal cells; M_2 and CuA_1 faded prior to wing margin; cell cu*p* longer than cell bm; CuA_2 convex.

Legs yellowish-brown, except mid and hind coxae tinged with black. Fore coxa slender, parallel-sided, lacking inner setae. Anterior basal spine-like seta of fore femur twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 12 spine-like posteroventral setae.

Abdomen. Sclerites thinly sclerotized and reduced in size. Hypandrium with crown of blunt, apical, spine-like setae. Posterior margin of epandrium irregular. Left surstylus elongate, cylindrical, bearing blunt, inner dorsal spine-like setae on basal half; right surstylus short, pointed, strongly held inwards. Right bacilliform sclerite elongate, bearing blunt, spine-like setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 24). Phallus with broad lateral, flexible cap.

Female. Similar to male except setae of foreleg more pronounced; fore tibia with 12–15 spine-like, posteroventral setae. Tergite 8 weakly sclerotized on lateral margin subapically, with Y-shaped, dorsoapical sclerite bearing several pairs of lateral setae (Fig. 10).

Distribution. Confined to high tablelands in the wet tropics region of northern Queensland near Cairns (Fig. 33).

Biology. Collected in cool, submontane rainforests (above 700 m).

Etymology. The specific name is derived from the Greek *pala* (gold nugget), in reference to the golden or orange colour of the thorax of this species.

Apterodromia setosa n.sp.

Figs. 25, 36

Material examined. HOLOTYPE ♂, "AUST[ralia]: TAS[mania]: Mt. Field/ N.P. Lyrebird Tr./ 17–19.ii.1994, 700m/ ex. yellow pans/ B.J. Sinclair"; "HOLOTYPE/ Apterodromia/ setosa/ Sinclair & Cumming [red label]" (AMS).

Additional material. TASMANIA: ♀, Mt. Rufus, Lk. St. Clair NP, 29.iv.1987, berlese litter from beech eucalyptus for., N.I. Platnick *et al.* (AMNH). This is possibly conspecific, but an associated male specimen is required for confirmation.

Diagnosis. Distinguished from the other apterous species by its reddish-brown forelegs, yellowish tubercles at base of fore femur, and long setae on inner and outer faces of the surstyli and right bacilliform sclerite.

Description. Body length 2.0–2.5 mm.

Male. *Head*. Scape and pedicel yellowish-brown; first flagellomere and arista dark brown; first flagellomere pointed ovate.

Thorax entirely black. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite black.

Wings. Absent. Halter absent.

Legs. Fore coxa pale yellow; lacking inner setae. Fore femur reddish-brown, basal half of posterior surface becoming darker basally, tubercles of basal setae yellow; not strongly attenuated apically; anterior basal spine-like seta less than twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 9 spine-like posteroventral setae. Fore tibiae reddish-brown, tarsal segments dull brown. Mid and hind coxae yellowish-brown, becoming black basally. Mid and hind femora with broad brown band on basal half, more distinct on hindleg; remaining leg segments yellowish-brown gradually darkening on tarsal segments.

Abdomen. Sclerites heavily sclerotized (except sternites 1 and 2 which are weakly sclerotized); tergites 1 and 2 immovably fused together with intersegmental suture still obvious at lateral margin. Hypandrium with scattered, pointed, stout setae near apex, right apicolateral margin with deep U-shaped notch. Posterior margin of epandrium deeply cleft, rectangular. Left surstylus elongate, cylindrical, bearing long, setae on outer margin, equal to half length of lobe; right surstylus slightly more than half length of left surstylus, blunt, geniculate near base, bearing long setae along outer margin. Right bacilliform sclerite elongate, bearing very long, slender setae along upper half. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 25). Phallus with small oval flexible cap.

Female. Similar to male except banding of mid and hind legs less distinct. Tergite 8 sclerotized along entire margin, not subdivided apically.

Distribution. Know with certainty only from the holotype which was collected in yellow pans at an altitude of 700 m (Fig. 36).

Biology. The holotype of this species was collected in cool, moist forest with upper canopy of *Eucalyptus* sp. and lower canopy of *Nothofagus cunninghami*.

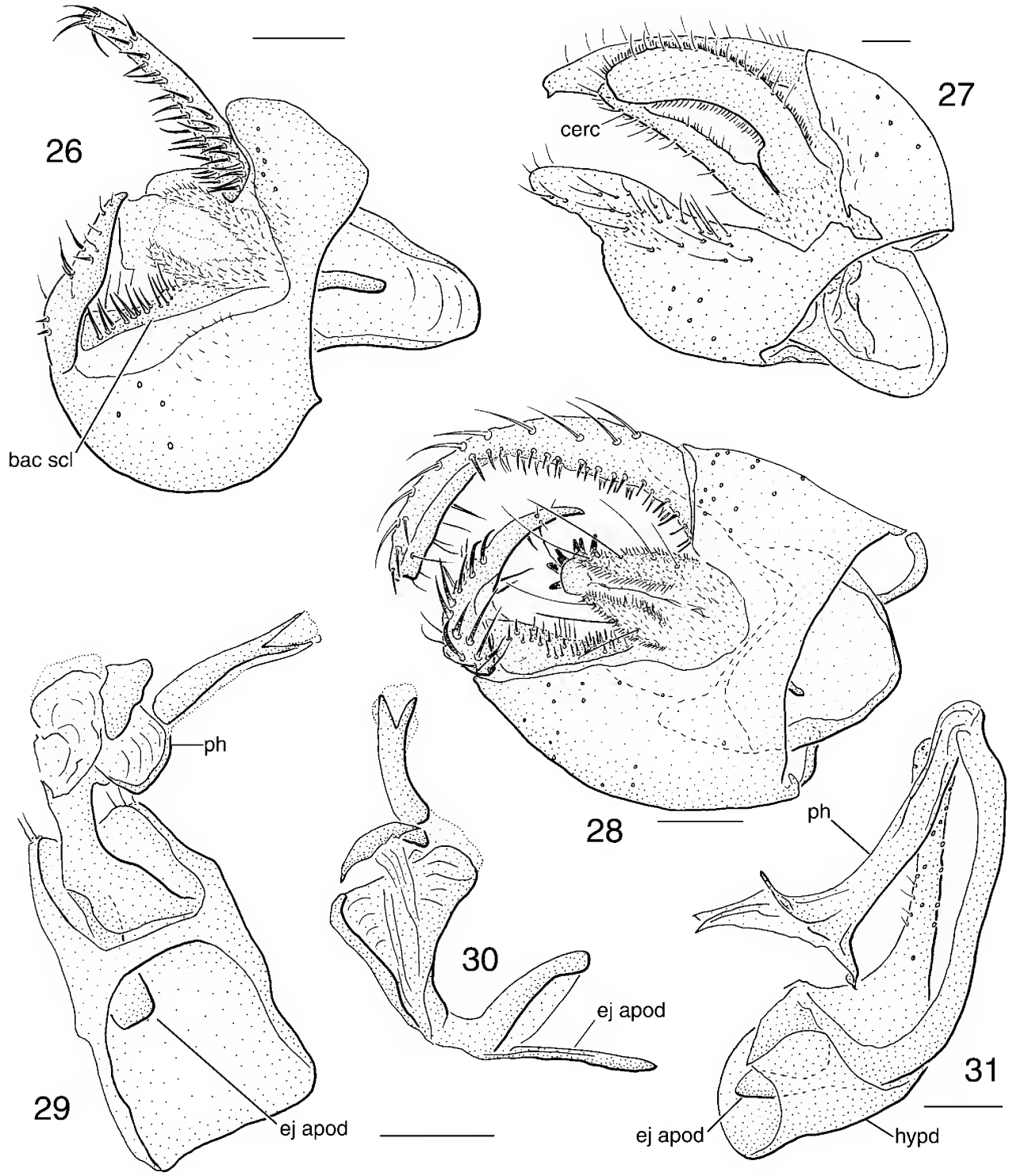
Etymology. The specific name is derived from the Latin *setosus*, meaning bristly, in reference to the long setae on the surstylus and right bacilliform sclerite.

Apterodromia spilota n.sp.

Figs. 5, 35

Material examined. HOLOTYPE ♀, "Hellyer River/ Gorge, NW Tas.[mania]/ 9.Feb.1971/ A. Neboiss"; "HOLOTYPE/ Apterodromia/ spilota/ Sinclair & Cumming [red label]" (MVM).

Diagnosis. Distinguished from all other winged species of *Apterodromia* by clouding surrounding the crossveins,



Figures 26–31. Male terminalia. 26, *Apterodromia tasmanica*, dorsal view. 27, *A. tonnoiri*, dorsal view. 28, *A. vespertina*, dorsal view. 29. *Leptodromia bimaculata*, hypandrium and phallus, dorsal view. 30, *L. bimaculata*, phallus, lateral view. 31, *Neotrichina* sp., hypandrium and phallus, oblique lateral view. Scale bars = 0.1 mm. Abbreviations: bac scl, bacilliform sclerite; cerc, cercus; ej apod, ejaculatory apodeme; hypd, hypandrium; ph, phallus.

presence of a ventral row of spine-like setae on the fore femur and an inner row of short stout setae on the fore coxa.

Description. Body length 4.5 mm.

Female. *Head*. Scape, pedicel, first flagellomere and arista dark brown; first flagellomere conical.

Thorax dark brown. Proepisternum with 2 spine-like setae above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite brown.

Wing (Fig. 5) infuscate; basal costal seta lacking; dark cloudy patches surrounding crossveins and tips of major veins. Costa fading beyond M_1; auxiliary crossveins between costa and R_{2+3} and R_{2+3} and R_{4+5}; cell dm broad, shorter than cell bm; M_2 and CuA_1 reaching wing margin; cell cu*p* short, two-thirds length of cell bm; CuA_2 straight.

Legs yellowish-brown. Fore coxa slender, with inner row of short, stout setae. Anterior basal spine-like seta of fore femur equal in length to posterior spine-like seta; armed beneath with row of 8 spine-like setae mounted on short tubercles. Fore tibia with 12 spine-like posteroventral setae.

Abdomen. Sclerites brown, well sclerotized. Tergite 8 sclerotized along entire margin, not subdivided apically.

Male. Unknown.

Distribution. This species is known from only the type locality in northwestern Tasmania (Fig. 35).

Etymology. The specific name is derived from the Greek *spilotos*, meaning spotted, in reference to the dark cloudy patches on the wing.

Apterodromia tasmanica n.sp.

Figs. 26, 36

Material examined. HOLOTYPE ♂, "[Australia] 42.40S 145.58E/ Southwest Tasmania/ 19.iii.1976/ C. Howard, litter"; "HOLOTYPE/ Apterodromia/ tasmanica/ Sinclair & Cumming [red label]" (ANIC). ALLOTYPE ♀, "[Australia] 42.35'S 145.42'E/ Southwest Tasmania/ 29.i.1976/ C.Howard, litter"; "ALLOTYPE/ Apterodromia/ tasmanica/ Sinclair & Cumming [red label]" (ANIC). PARATYPE: TASMANIA: ♂, 42°40S 145°58E, 19.iii.1976, C. Howard, litter (ANIC).

Diagnosis. Distinguished from other apterous species by the yellowish-brown fore femur (which is evenly pigmented along its entire length), the lighter coloured (brown) first flagellomere, and long, slender right surstylus. The male terminalia are also characterized by long (subequal in length to width of surstylus) tapering, spine-like setae along the entire length of the left surstylus and the apical half of the right bacilliform sclerite.

Description. Body length 1.5–2.0 mm.

Male. *Head*. Scape and pedicel yellowish brown; first flagellomere and arista brown; first flagellomere pointed ovate.

Thorax entirely black. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite black.

Wings. Absent. Halter absent.

Legs. Fore coxa pale yellow-brown; lacking inner setae. Fore femur entirely yellowish-brown, not strongly attenuated apically; anterior basal spine-like seta less than twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 6–8 spine-like posteroventral setae. Fore tibia and tarsomeres yellowish-brown. Mid and hind coxae yellow to brown, gradually darkening to black basally. Mid and hindlegs yellowish-brown.

Abdomen. Sclerites heavily sclerotized (except sternites 1 and 2 which are weakly sclerotized); tergites 1 and 2 immovably fused together with intersegmental suture still obvious at lateral margin. Hypandrium with scattered, pointed, stout setae near apex. Posterior margin of epandrium deeply cleft, V-shaped. Left surstylus elongate, narrow and cylindrical, bearing long, tapering setae on inner dorsal margin near base; right surstylus greater than half length of left surstylus, tapered, slightly geniculate near base, bearing short setae. Right bacilliform sclerite elongate, bearing long, spine-like setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 26). Phallus with small subrectangular cap.

Female. Similar to male except fore tibia with row of 9 spine-like posteroventral setae. Tergite 8 sclerotized along entire margin, not subdivided apically.

Distribution. Currently known only from southwestern Tasmania (Fig. 36).

Biology. This species was collected in litter samples.

Etymology. Refers to the distribution of this species, which is restricted to Tasmania.

Apterodromia tonnoiri n.sp.

Figs. 6, 27, 36

Material examined. HOLOTYPE ♂, "Tasm[ania]./ Launceston/ 15.x.1933, A. Tonnoir" (ANIC). "HOLOTYPE/ Apterodromia/ tonnoiri/ Sinclair & Cumming [red label]" (ANIC).

Diagnosis. Distinguished from all other winged species of *Apterodromia* by clouding surrounding the crossveins, presence of a ventral row of spine-like setae on the fore femur, and lack of inner row of stout setae on the fore coxa. The male terminalia appear unique (not known for the closely related *A. spilota*), characterized by a posteriorly directed epandrial lobe that covers the right surstylus, and elongate heavily sclerotized, asymmetrical cerci.

Description. Body length 4.0 mm.

Male. *Head*. Scape, pedicel, first flagellomere and arista dark brown; first flagellomere conical.

Thorax dark brown, nearly black. Proepisternum with 2 spine-like setae above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite dark brown.

Wing (Fig. 6) infuscate; basal costal seta lacking; dark cloudy patches surrounding crossveins, M_1, and tips of major veins. Costa fading beyond M_1; auxiliary crossvein between costa and R_{2+3}, but not between R_{2+3} and R_{4+5}; cell dm broad, slightly shorter than cell bm; M_2 and CuA_1 reaching wing margin; cell cu*p* short, two-thirds length of cell bm; CuA_2 straight.

Legs brown. Fore coxa slender, lacking inner row of short, stout setae. Anterior basal spine-like seta of fore femur equal in length to posterior spine-like seta; armed beneath with row of 9 spine-like setae mounted on short tubercles. Fore tibia with 12 spine-like posteroventral setae.

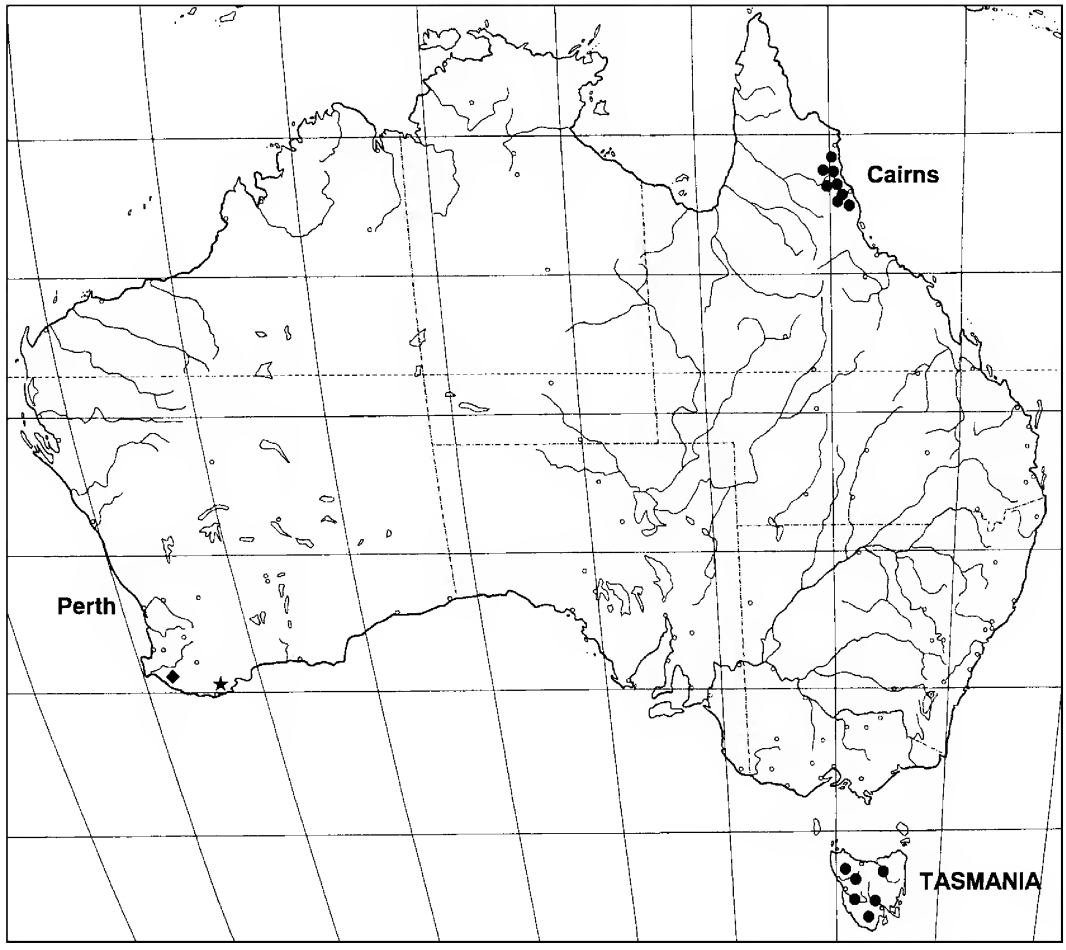


Figure 32. Known distribution of species of *Apterodromia*. *Apterodromia* spp, eastern (●), *A. irrorata* (◆), *A. vespertina* (★).

Abdomen. Sclerites dark brown, well sclerotized. Hypandrium without stout or spine-like setae near apex. Posterior margin of epandrium ragged, with deep, narrow incision. Left surstylus elongate, lacking stout setae; right surstylus short, pointed, strongly held inwards (covered dorsally by posteriorly directed lobe of epandrium). Right bacilliform sclerite lacking stout setae. Cerci heavily sclerotized, asymmetrical, with left cercus expanded apically, curved over lower slender right cercus (Fig. 27). Phallus with subrectangular cap.

Female. Unknown.

Distribution. This species is known only from the type locality in northern Tasmania (Fig. 36).

Etymology. Named after A. Tonnoir, the collector of the single known specimen of this species.

Remarks. This species, which is known only from the male, is most closely related to *A. spilota*, which is known only from the female. However, the differences in setation of the fore coxae, wing venation, and wing patterning between these two are not indicative of conspecific secondary sexual characteristics observed in *Apterodromia*.

Apterodromia vespertina n.sp.

Figs. 28, 32

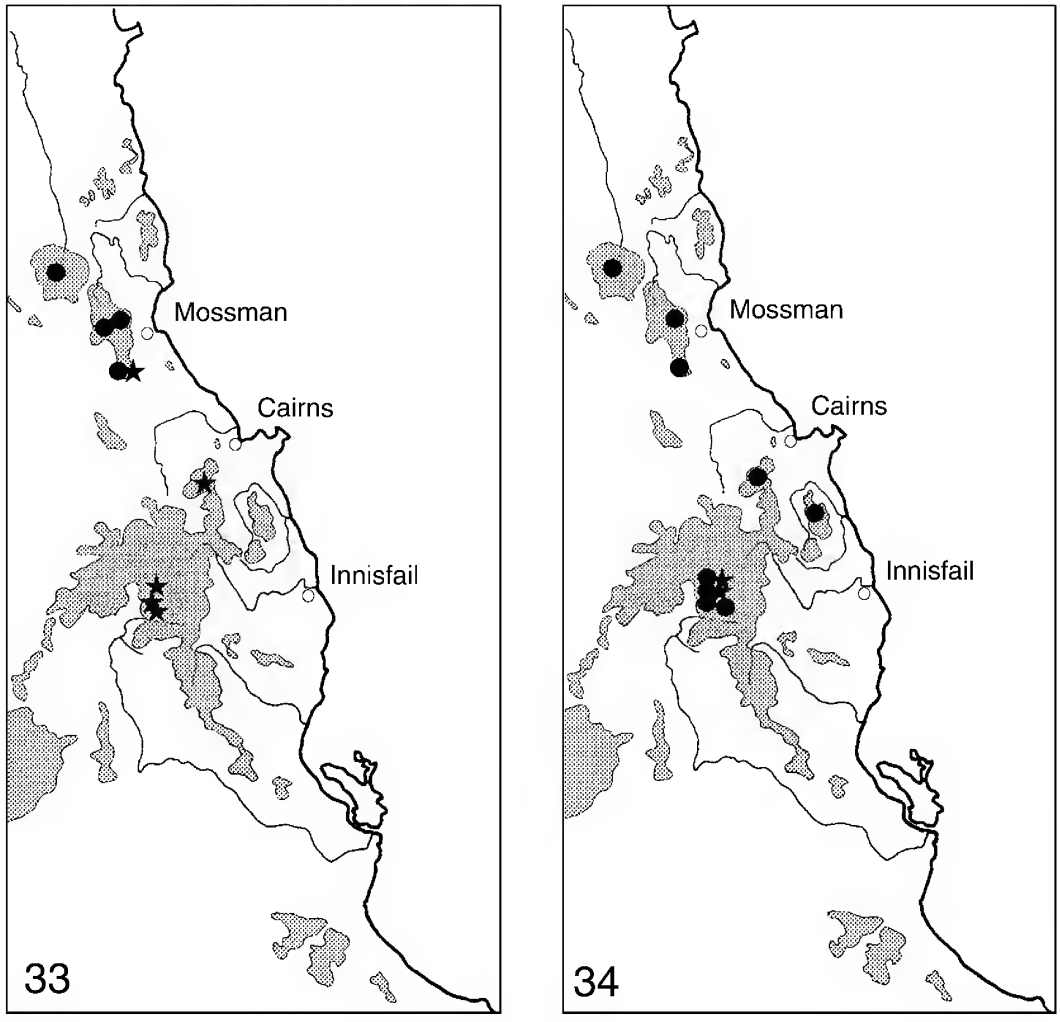
Material examined. HOLOTYPE ♂, "[AUST:WA]/ Porongorup NP, at Pass,/ Devil's Slide TR./ 4–5.Dec.1998/ B.J. Sinclair"; "HOLOTYPE/ Apterodromia/ vespertina/ Sinclair & Cumming [red label]" (WAM).

Diagnosis. Distinguished from all other winged species of *Apterodromia* by irrorated pattern on the wings, auxiliary crossvein from R_{2+3} to costa, and two spine-like proepisternal setae. The male terminalia are characterized by a very long, curved left surstylus with short setae on basal two-thirds and right bacilliform sclerite with slender setae.

Description. Body length 3.5 mm.

Male. *Head*. Scape, pedicel, first flagellomere and arista black; first flagellomere subtriangular. Vertex of head with median, brownish vitta from base of antennae to beyond occipital setae.

Thorax black. Proepisternum with 2 spine-like setae above fore coxa, upper one-quarter longer than lower; notopleural seta slender. Mesopleuron, metapleuron and mediotergite black.



Figures 33–34. Known distribution of species of *Apterodromia* in northern Queensland. 33, *A. aurea* (●), *A. pala* (★). 34, *A. bickeli* (●), *A. monticola* (★). Shaded areas indicate land above 700 m in altitude.

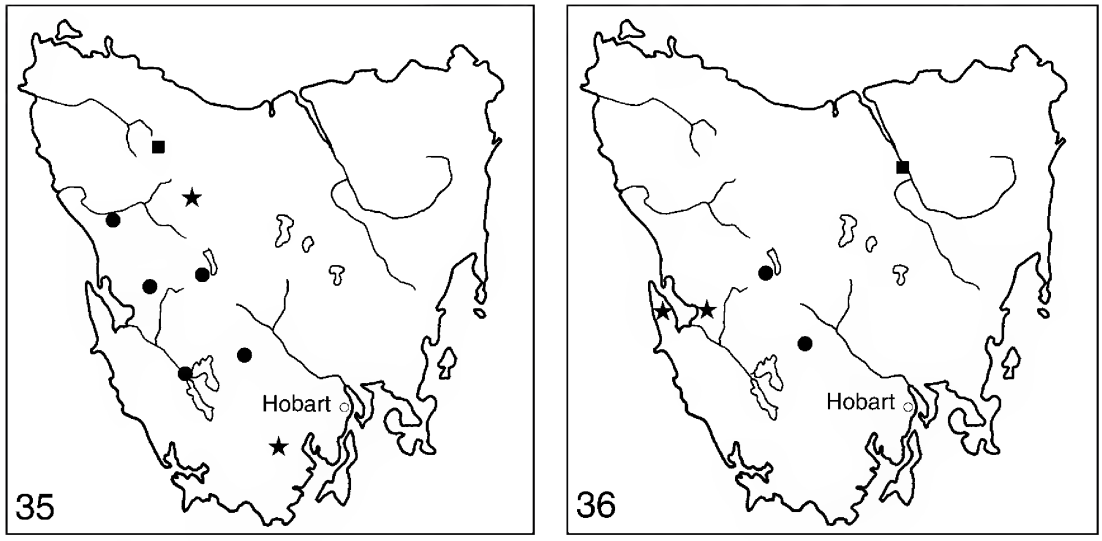
Wing infuscate; basal costal seta slender, short; veins weakly undulating; numerous pale spots or irrorations: cell r_1 with 3 broad spots, cell r_{2+3} with 5 round spots, cell r_{4+5} with ca. 12 spots, 3 spots in cell dm, 2 spots in cell m_1, cell m_2 with 1 large spot, cell cua_1 with 2 spots, cell cu*p* with 1 apical spot. Auxiliary crossvein between costa and R_{2+3}; cell dm narrow, ca. one-third longer than cell bm; M_2 and CuA_1 faded prior to wing margin; cell cu*p* longer than cell bm; CuA_2 convex.

Legs. Fore coxa brownish-yellow; lacking inner setae. Fore femur brown on posterior face, tubercles of basal setae yellow; femur not strongly attenuated apically; anterior basal spine-like seta ca. equal in length to posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 14–16 spine-like posteroventral setae. Fore tibia and first tarsomere yellowish brown, remaining tarsal segments dull brown. Mid and hind coxae brown, becoming black basally. Ventral surface of mid and hind femora with basal fourth yellowish, remaining femora brown, darker towards apex; remaining leg segments brown gradually darkening on tarsal segments.

Abdomen. Sclerites lightly sclerotized. Hypandrium with scattered, pointed, stout setae near apex. Posterior margin of epandrium deeply cleft, U-shaped. Left surstylus elongate, arching beyond right surstylus; cylindrical, outer margin with long setae and pile of setulae; inner dorsal margin with dense stout setae, extending two-thirds length of surstylus; apex truncate, slightly notched. Right surstylus more than half length of left surstylus, geniculate near base, bearing long, stout basal setae extending beyond middle on apical margin; tapered to narrow apex. Right bacilliform sclerite elongate, bearing short, stout setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 28). Phallus with oval flexible cap.

Female. Unknown.

Distribution. This species is known only from the type locality, a small eastern forest remnant, north of Albany (Western Australia), widely disjunct from the wet forests further west (Fig. 32).



Figures 35–36. Known distribution of species of *Apterodromia* in Tasmania. 35, *A. evansi* (★), *A. minuta* (●), *A. spilota* (■). 36, *A. setosa* (●), *A. tasmanica* (★), *A. tonnoiri* (■).

Biology. This specimen was collected along the edge of a seepage near the trail along Devil's Slide. This is an intermittent seepage, as it dries up during the summer months. No specimens were collected in the Karri forest situated below Devil's Slide.

Etymology. The specific name is derived from the Latin *vespertinus* (western), in reference to the distribution of this species in Western Australia.

Remarks. This species is most closely related to *A. irrorata*, with very similar male terminalia and wing pattern. However, it is considered a distinct species on the basis of its larger size, long, stout left surstylus arching beyond the right surstylus, stout setae of right surstylus extending well beyond base, two spine-like proepisternal setae, auxiliary crossvein present, and numerous small irrorations in cell r_{4+5}.

Evolutionary history

Zoogeographic considerations

Apterodromia is an example of a Bassian faunal element (Spencer 1896), modified to include the temperate and tablelands rising from the tropical and subtropical lowlands of Northern Queensland (Nix, 1991). The Bassian subregion has a moist temperate climate, with vegetation ranging from southern rainforests and wet sclerophyll to alpine herb fields (Mackerras, 1970). Nix (1991) referred to the "islands" of cool, moist mountains in eastern Queensland as a mesotherm archipelago defined by a broad group of plants that have optimum temperatures for growth of 19–22°C, with a lower threshold of 5°C. These regions above 400 m are isolated from the mesotherm source area of southern Australia by warm temperatures and low rainfall (Nix, 1991, fig. 15). Although *Apterodromia* displays a Bassian pattern, this genus must be considered a relict taxon on the basis of the widely disjunct species. It is a remnant associated with widespread Tertiary vegetation and the zoogeographic pattern is the result of extinction rather than speciation. The geographic distribution of *Apterodromia* is equivalent to many Gondwanan taxa and it is possible that with further collections using yellow pans that this genus may be recorded from southern Chile and possibly New Zealand.

The northern extension of this genus (the Tablelands west of Cairns) is common in southern temperate groups; e.g., *Scaptia* Walker (Tabanidae, Mackerras, 1970). Darlington (1961) observed several genera of the tribe Trechini (Carabidae) common in temperate southern Australia, whereas in the tropics these genera were confined to the Atherton Tableland (+600 m). Darlington assumed this distribution pattern was the result of ecological factors (e.g., cooler temperatures).

The disjunct pattern in eastern Australia (Northern Queensland and Tasmania) is also observed in the empidid genus *Hydropeza* Sinclair (Sinclair, 1999). In addition, Queensland Tablelands-Tasmania sister species pairs are known in *Clinocera* Meigen (Sinclair, 2000) and *Ceratomerus* Philippi (Sinclair, unpublished data).

Apterodromia is also characterized by high endemism in Tasmania, where a total of six species are recorded. In *Ceratomerus*, a genus generally confined to cool, moist forests and mountain streams, five of seven Tasmanian species are endemics (Sinclair, unpublished data). High Tasmanian endemism is also known in the aquatic orders Odonata, Plecoptera, and Trichoptera (Watson & O'Farrell, 1991; Hynes, 1976; Neboiss, 1991). The Odonata include several endemic cold-water genera, suggesting long isolation of stream faunas (Watson & O'Farrell, 1991). It can be assumed that the wet forests of Tasmania have also undergone a long period of isolation dating from middle Miocene when conditions on the continent started to become much drier (White, 1994). Although Tasmania was connected to the mainland during the Pleistocene, the land bridges were primarily low plains, providing routes primarily for lowland, warm adapted species (Hynes, 1976; White, 1994).

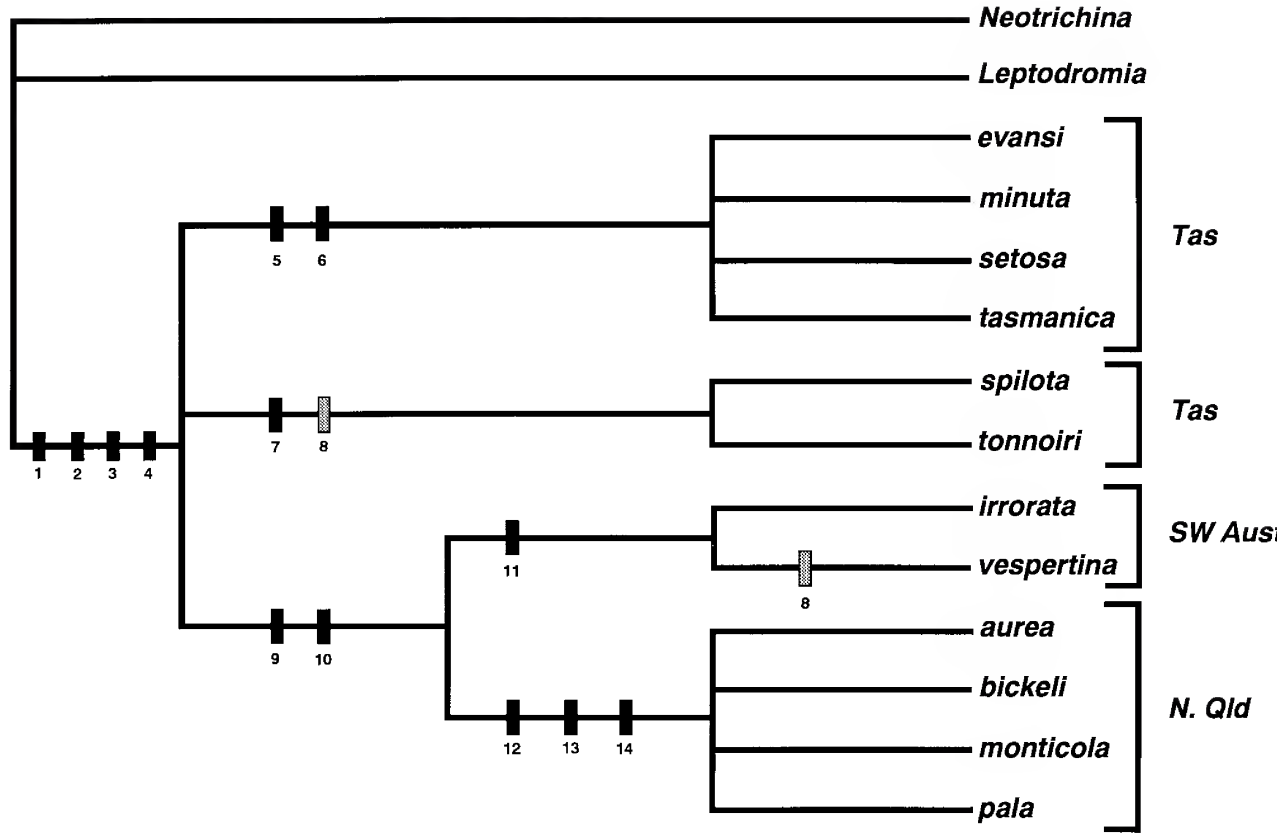


Figure 37. Hypothesized cladistic relationships of the species of *Apterodromia*. Numbers refer to characters discussed under "Phylogenetic relationships within *Apterodromia*". Black rectangles = non-homoplastic apomorphies; shaded rectangles = homoplastic apomorphies. Abbreviations: N. Qld—Northern Queensland; SW Aust—Southwestern Australia; Tas—Tasmania.

Phylogenetic position of *Apterodromia*

Oldroyd (1949) referred *Apterodromia* to the hybotid group of subfamilies or hybotid lineage (= Hybotidae sensu Chvála, 1983), specifically the subfamily Tachydromiinae. However, without male specimens, this placement has been doubted (Cumming, unpublished data). The discovery of both males and fully winged species of this genus has allowed us to analyse the subfamily placement with much more confidence.

On the basis of current subfamily and tribal divisions, the combination of a long arista, cell dm present and emitting three veins, simple hindlegs, and a single ejaculatory apodeme, suggests that this genus should be transferred to the Trichinini (Ocydromiinae). However, the above characters are symplesiomorphies and this tribe generally includes taxa that do not fit into any other lineage as currently defined (see below).

It could be also argued that the elongate cell cu*p* (anal cell) resembles some Hybotinae, in contrast to the short, truncate cell cu*p* common in the Ocydromiinae. Although the cell cu*p* resembles some species of *Syneches* Walker (Smith, 1969, fig. 110), this probably represents the ground plan condition of the hybotid lineage. Especially when compared to relevant outgroups such as *Meghyperus* Loew (Steyskal & Knutson, 1981, fig. 47.17) and allied fossil empidoids like *Phaetempis* Grimaldi & Cumming (1999, fig. 32) and *Trichinites* Hennig (1970, fig. 3).

In an effort to avoid possible homoplasy through the interpretation of wing venation, we believe the main clues to the most plausible placement of *Apterodromia* is through the interpretation of the male terminalia. On the basis of a biarticulated phallus (apical articulated component or distiphallus), posterior margin of the hypandrium not deeply cleft, and absence of both postgonites and ventral apodeme (see Cumming & Sinclair, 1996; Sinclair, 1996), *Apterodromia* is herein transferred to the tribe Ocydromiini. A comparison of the genitalic figures of Collin (1961, figs. 93–5) and Chvála (1983, figs. 543–546, 553–555) illustrates the uniformity of the male terminalia in this tribe. In order to incorporate the inclusion of *Apterodromia*, the concept of the Ocydromiini is redefined below and included genera listed. A key to genera of Ocydromiini of the Southern Hemisphere is also included to aid identification.

The generic relationships within the Ocydromiini have not been analysed. The most plesiomorphic genus of this tribe appears to be *Neotrichina* n.gen. (see below) which has retained holoptic male eyes, with enlarged upper facets and three veins arising from cell dm that extend to the wing margin. On the basis of the configuration of the phallus, *Apterodromia* is hypothesized to be most closely related to an undescribed genus represented by "*Leptopeza*"

bimaculata White (1916) (*Leptodromia* n.gen., see below). The apex of the shaft of the phallus below the articulated apex is expanded or cup-shaped in both genera (c.f. Figs. 18, 29). All other genera appear to have a long, slender phallic shaft (Fig. 31), which is probably derived in comparison to the remaining groups in the hybotid lineage.

Phylogenetic relationships within *Apterodromia*

The relationships within *Apterodromia* were analysed using PAUP Version 4.0b2 (Swofford, 1999) based on 14 informative characters (matrix in Table 1), with *Neotrichina* n.gen. and *Leptodromia* n.gen. (see below) used as outgroups. A heuristic search was performed, with stepwise addition resulting in one tree (Fig. 37) (tree length = 15; CI = 0.93; RI = 0.97; RC = 0.91).

Apterodromia is a distinctly monophyletic taxon within the Ocydromiini on the basis of the following characters: eyes with dense ommatrichia, fore femur with pair of long spine-like basal setae, fore tibia with ventral spine-like setae, and proepisternum with one spine-like seta (characters 1–4).

The apterous species of Tasmania are hypothesized to form a monophyletic group based on the loss of wings (character 5) and a modification of the base of the abdomen (character 6). In these species tergites 1 and 2 are immovably fused to form a plate over sternites 1 and 2, which are both virtually desclerotized and almost entirely membranous. Another character that may support this subgroup is a very narrow dorsal bridge connecting the two epandrial halves. It appears generally more slender compared to the winged species.

A row of spine-like setae on the fore femur and pair of proepisternal spines (characters 7 and 8) indicate the close relationship of the two fully-winged Tasmanian species. In addition, both species possess clouding along the crossveins of the wings that may also support this relationship, although at least some degree of wing clouding is present in the other winged species of *Apterodromia*. A pair of proepisternal spines (character 8) appears to have arisen in *A. vespertina* independently from those seen in the fully-winged Tasmanian species.

A convex CuA_2 and a lightly or weakly sclerotized abdomen (characters 9 and 10) support the sister group relationship between the western species group (*A. irrorata* and *A. vespertina*) and the northern Queensland species group. All Tasmanian species (i.e., winged and wingless) and outgroup taxa have well sclerotized abdomens. The western species group is considered monophyletic on the basis of irrorated wings (Fig. 3) (character 11). The four species found in Northern Queensland form a monophyletic group on the basis of blunt spines on the right bacilliform sclerite and left surstylus (Figs. 11, 14, 23, 24), an elongate cell dm (twice length of basal cells, Fig. 4), and a small dorsoapical sclerite partially separated from the apical margin of tergite 8 in the female terminalia (Figs. 8, 10) (characters 12–14).

Table 1. Data matrix of character states for the phylogenetic analysis of species of *Apterodromia*. Character numbers correspond to those in the text. 0, plesiomorphic state; 1, apomorphic state; ?, missing data; –, inapplicable (structure absent).

	characters													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Neotrichina	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptodromia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
evansi	1	1	1	1	1	1	0	0	0	0	–	0	–	0
minuta	1	1	1	1	1	1	0	0	0	0	–	0	–	0
setosa	1	1	1	1	1	1	0	0	0	0	–	0	–	0
tasmanica	1	1	1	1	1	1	0	0	0	0	–	0	–	0
spilota	1	1	1	1	0	0	1	1	0	0	0	?	0	0
tonnoiri	1	1	1	1	0	0	1	1	0	0	0	0	0	?
irrorata	1	1	1	1	0	0	0	0	1	1	1	0	0	0
vespertina	1	1	1	1	0	0	0	1	1	1	1	0	0	?
aurea	1	1	1	1	0	0	0	0	1	1	0	1	1	1
bickeli	1	1	1	1	0	0	0	0	1	1	0	1	1	1
monticola	1	1	1	1	0	0	0	0	1	1	0	1	1	1
pala	1	1	1	1	0	0	0	0	1	1	0	1	1	1

Ocydromiini

Type genus: *Ocydromia* Meigen

The tribe includes the following genera: *Abocciputa* Plant, *Apterodromia* Oldroyd, *Austropeza* Plant, *Hoplopeza* Bezzi, *Leptodromiella* Tuomikoski, *Leptopeza* Macquart, *Ocydromia* Meigen, *Oropezella* Collin, *Pseudoscelolabes* Collin, *Scelolabes* Philippi, *Stylocydromia* Saigusa, plus all Neotropical species of *Trichina* sensu Collin (1933) and *Leptopeza bimaculata* Bezzi which are assigned to two new genera described below.

Diagnosis. This tribe is distinguished from the other major clades of the hybotid lineage by a short cell cu*p* with truncate apex (except some *Apterodromia*), arista subequal or much longer than the first flagellomere, proboscis short, directed downwards or recurved, terminalia asymmetrical, rotated through 90°, phallus biarticulated, ventral apodeme and postgonites lacking, and epandrium with a pair of articulated surstyli.

Description

Male. *Head*. Eyes widely separated or closely approximated to holoptic; upper facets rarely enlarged. Antenna with small first flagellomere with style arista-like. Proboscis short, directed downwards; labrum and hypopharynx strongly arched at apex; pseudotracheae present.

Thorax. Slightly to strongly arched; acrostichal setulae usually present.

Wings. Costa generally ending at R_{4+5} or M_1; cell dm emitting 2 or 3 veins, or short stump of M_1; cell cu*p* shorter than basal cells and apex truncate or longer than basal cells and apex convex.

Legs. Hindlegs generally elongate with variable chaetotaxy.

Abdomen. Terminalia asymmetrical, rotated through 90°; surstylus clearly articulated, asymmetrical; hypandrium with posterior margin not deeply cleft, lacking pair of apical lobes; phallus with long, flexible terminal appendage or

distiphallus; postgonites and ventral apodeme lacking; ejaculatory apodeme single.

Female. Similar to males except as follows: eyes similar to males, but not holoptic. Terminalia variable, with slender terminal cercus. Spermatheca unpigmented, simple, weakly sclerotized, slender, and tubular.

Discussion. As listed by Sabrosky (1999) the family-group name was first established by Schiner (1862) as Ocydrominae, with the suffix later corrected by Melander (1908) to Ocydromiinae. Tuomikoski (1966) was the first to attempt to classify the subfamily into three monophyletic groups of genera. From these groupings, Chvála (1983) formally defined and characterized the tribe Ocydromiini.

With the inclusion of *Apterodromia* in the Ocydromiini, the only significant change in the present tribal definition is that cell dm emits three veins that reach the wing margin in the ground plan of the tribe. The Chilean and Patagonian species treated by Collin (1933) as *Trichina* Meigen are not congeneric with the northern hemisphere *Trichina* (Trichinini). These southern hemisphere species are also included in the Ocydromiini under a new genus (*Neotrichina*, see below), on the basis of the characteristic biarticulated phallus (Fig. 31; Collin, 1933, fig. 9).

Presence of a biarticulated phallus, plus loss of both the postgonites and ventral apodeme substantiates the monophyly of the Ocydromiini as currently defined. The relationships of the tribe to the remainder of the Ocydromiinae and the other subfamilies in the hybotid lineage (i.e., Hybotinae and Tachydromiinae) can only be partially resolved at present. Cumming *et al.* (1995, fig. 1) indicated that the Ocydromiinae is paraphyletic in relation to both the Hybotinae and Tachydromiinae. Using the Atelestinae as an outgroup, the Hybotinae (including *Bicellaria* Macquart, *Hoplocyrtoma* Melander, and *Leptocyrtoma* Saigusa), Tachydromiinae, Oedaleini, *Trichinomyia* Tuomikoski and *Trichina* appear to form a monophyletic group on the basis of two synapomorphies (Sinclair & Cumming, 1994; Cumming & Sinclair, 1996). The first is a modification of the ventral apodeme in which the separate paired rods seen in the Atelestinae appear to have fused together (see Sinclair, 1996, fig. 23), and the second is a modification of the phallus in the ground plan of each included lineage into a hood-like tip. The Ocydromiini by exclusion is therefore possibly the sister group to this diverse clade.

The Ocydromiini in distributed worldwide, and is the only tribe of the "Ocydromiinae" represented in southern South America, Australia, and New Zealand.

Neotrichina n.gen.

Type species: *Trichina obscurata* Collin, 1933.

Diagnosis. Distinguished from all other genera of the Ocydromiini by three veins arising from cell dm reaching the wing margin, upper facets of male enlarged, and a long flexible distiphallus extending nearly the length of the shaft.

Description. Wing length 3.5–4.5 mm.

Male. *Head* dark, with extensive pruinescence. Eye bare, holoptic, upper facets enlarged. Face parallel-sided, width equal to antennal sockets. Gena not extended below eye; postgena with sparse setae. Two pairs of fine ocellar setulae, directed forward. One pair of vertical and 1–2 pairs of upper occipital setae. Antennae inserted about middle of head; scape and pedicel subequal in length, scape devoid of setulae; pedicel cylindrical, with circlet of short preapical setae; first flagellomere tapered to narrow apex, less than 2 times length of first and second segments combined; two-articled apical arista variable in length; first flagellomere and arista clothed in fine pubescence. Palpus tapered and flattened, pale, one-half to two-thirds length of proboscis; length of proboscis normally less than half height of head. Mouthparts as in other ocydromiines.

Thorax polished to thickly clothed in pruinescence; dark to orange-yellow in colour, occasionally with dark markings; slightly to strongly arched, postpronotal lobe and postalar callus well developed; prosternum separate from proepisternum; proepisternum with fine setae; antepronotum well developed, forming wide "neck"-like extension. Thoracic macrotrichia mostly slender and short; acrostichal setulae biserial, confined to anterior half; dorsocentral setulae uniserial; 1 postpronotal setula; 1 notopleural seta; 1 postalar seta; 1 pair of long, apical scutellar setae, with several pairs of outer marginal setulae. Meso- and metapleuron with patches of pruinescence.

Wings hyaline, broad, anal lobe well developed; microtrichia of equal length; costal setae short; basal costal seta short; costa fading beyond M_1; Sc evanescent, extending to beyond R_{2+3} and R_{4+5} branching; stigma overlapping apex of R_1, occasionally extending to tip of R_2; Rs long, arising proximal to middle of cell bm; cell dm broad, subequal to or longer than cell bm; 3 veins emitted from cell dm, each obtaining wing margin; cell cu*p* approximately two-thirds or more length of cell bm. Halter pale to dark.

Legs yellow to dark; long and slender; some species with hind tibia dilated at apex and first and second tarsomeres dilated. Fore coxa short, less than twice length of other coxae; clothed in long, pale setae. Fore tibia with tubular gland near base. Femora and tibiae lacking stout anterodorsal and posterodorsal setae.

Abdomen. Tergites heavily sclerotized, darkly polished. Sternites less sclerotized, and generally more pale. Sclerites of segment 8 not fused, approximately one-third length of preceding segment. Hypopygium asymmetrical, rotated approximately 90° to right. Hypandrium short, quadrate, posterior margin either shallowly bilobed or lengthened into long slender process (Fig. 31); dorsal bridge V-shaped. Epandrium deeply cleft, strongly asymmetrical; right surstylus slender, generally strongly arched; right surstylus short to long, occasionally strongly arched. Bacilliform sclerites short, bearing several setae. Cercus unmodified, short, slender and thinly sclerotized. Phallic shaft long, gradually arched, cylindrical, not expanded apically; distiphallus bearing small cap membranously lengthened to near length of shaft; ejaculatory apodeme fused to base of phallus.

Female. Similar to male except as follows: eyes dichoptic, all facets of equal size; frons widely divergent; tergites 1 and 2 not fused; segments 1–7 broad, wider than long,

gradually tapered; tergites slightly more thickly sclerotized than sternites; sclerites of segment 8 separate, similar in length to preceding segment, not ovipositor-like; sclerites of segment 10 small triangular in shape, divided medially; cercus long and slender, well sclerotized, bearing long scattered setae.

Distribution. This genus is confined to southern South America, currently recorded from Argentina and Chile.

Included species. The genus includes all Neotropical species previously treated by Collin (1933) under *Trichina*, namely *Neotrichina abdominalis* (Collin) **n.comb.**, *Neotrichina digna* (Collin) **n.comb.**, *Neotrichina digressa* (Collin) **n.comb.**, *Neotrichina distincta* (Collin) **n.comb.**, *Neotrichina elegans* (Bigot) **n.comb.**, *Neotrichina fida* (Collin) **n.comb.**, *Neotrichina indiga* (Collin) **n.comb.**, *Neotrichina insignis* (Collin) **n.comb.**, *Neotrichina insons* (Collin) **n.comb.**, *Neotrichina laeta* (Collin) **n.comb.**, *Neotrichina media* (Collin) **n.comb.**, *Neotrichina obscurata* (Collin) **n.comb.**. The authors examined specimens of these species housed in the CNC, whereas the type specimens are located in the BMNH.

Remarks. The Neotropical species of this genus have long been considered not to be congeneric with *Trichina*, as first noted by Tuomikoski (1959) and later by Collin (1961) and Chvála (1983).

Neotrichina can be separated into two groups as delineated by Collin (1933). The first includes *N. digna* and allied species, characterized by a long straight labrum, weakly arched thorax, and hind tibia dilated towards tip, with partially dilated first and second tarsomeres. The second includes *N. obscurata* and allied species, characterized by a shorter, less conspicuous labrum, strongly arched thorax, and slender legs.

Leptodromia n.gen.

Type species: *Leptopeza bimaculata* Bezzi, 1904.

Diagnosis. Distinguished from other genera of the Ocydromiini by a very short M_1, antennae inserted above middle of head, weakly developed anal lobe, and a long Rs vein.

Description. Wing length 3.5–4.5 mm.

Male. *Head* polished black. Eye bare, narrowly separated, all facets equally small. Face closely approximated; frons parallel-sided twice width of face. Gena not extended below eye; postgena with sparse setae. Two pairs of fine ocellar setulae, directed forward. One pair of vertical and 1–2 pairs of upper occipital setae. Antennae inserted above middle of head; scape and pedicel subequal in length, scape devoid of setulae; pedicel cylindrical, with circlet of short preapical setae; first flagellomere long and tapering to narrow apex, often 3 times length of first and second segments combined; two-articled apical arista nearly equal in length to first flagellomere; first flagellomere and arista clothed in fine pubescence. Palpus broad and flattened, pale, two-thirds length of proboscis; length of proboscis less than half height of head. Mouthparts as in other ocydromiines.

Thorax polished orange-yellow, often with dark markings; not strongly arched, postpronotal lobe and postalar callus well developed; prosternum separate from proepisternum; proepisternum bare or with setulae; antepronotum well developed, forming wide "neck"-like extension. Thoracic macrotrichia mostly slender and short; acrostichal setulae biserial, confined to anterior half; dorsocentral setulae uniserial; 1 postpronotal setula; 1 notopleural seta; 1 postalar seta; 1 pair of long, apical scutellar setae, with several pairs of outer marginal setulae. Pruinescence confined to lateral margins; meso- and metapleuron generally devoid of pruinescence, except on laterotergite.

Wings hyaline to infuscate, narrow, anal lobe weakly developed; microtrichia of equal length; costal setae short; basal costal seta long; costa fading beyond R_{4+5}; Sc evanescent, extending to beyond R_{2+3} and R_{4+5} branching; stigma at apex of cell r_1; Rs long, arising near middle of cell bm; cell dm broad, shorter than cell bm; M_1 short, abruptly ending well before wing margin; cell cu*p* approximately two-thirds length of cell bm. Halter pale.

Legs yellow to brown; long and slender, hind femur often with dark subapical band. Fore coxa short, less than twice length of other coxae; clothed in long, pale setae. Fore tibia with tubular gland near base. Femora and tibiae with stout, dark anterodorsal and posterodorsal setae.

Abdomen. Tergites heavily sclerotized, darkly polished. Sternites thinly sclerotized, pale. Sclerites of segment 8 not fused, approximately one-third length of preceding segment. Hypopygium asymmetrical, rotated approximately 90° to right. Hypandrium short, quadrate, posterior margin shallowly bilobed; dorsal bridge well sclerotized (Fig. 29). Epandrium deeply cleft, not strongly asymmetrical; right surstylus elongate, cylindrical, bearing setae; right surstylus short, more strongly arched. Bacilliform sclerites elongate, bearing several setae. Cercus unmodified, short, slender and thinly sclerotized. Phallic shaft short, expanded apically to form cup-shaped tip, bearing flexible cap and subapical process; ejaculatory apodeme fused to base of phallus (Figs. 29, 30).

Female. Similar to male except as follows: tergites 1 and 2 fused; segments 1–7 broad, wider than long; tergites heavily sclerotized and polished; sternites pale, thinly sclerotized; sclerites of segments 7 narrowly separated (appearing fused in dried specimens); sclerites of segment 8 separate, very slender, ovipositor-like, longer than 2 preceding segments; sclerites of segment 10 small triangular in shape, divided medially; cercus long and slender, well sclerotized, bearing long scattered setae.

Distribution. This genus is presently known only from Australia, widely distributed in wet eastern forests from Tasmania to northern Queensland and wet forests of southwestern Western Australia. Specimens are readily collected by sweep net or yellow pans.

Included species. The genus currently includes *Leptodromia bimaculata* (Bezzi) **n.comb.** from eastern Australia (NSW) and several undescribed species.

Key to Southern Hemisphere Ocydromiini[1]

1 Wings absent (Australia) ..... *Apterodromia* (in part)

—— Wings present 2

2 Cell dm lacking (Australia and Argentina) ..... undescribed genus A

—— Cell dm present 3

3 Three veins emitted from cell dm reaching wing margin 4

—— Two or fewer veins emitted from cell dm reaching wing margin 5

4 Fore femur greatly swollen, with 2 long basal spine-like setae (Australia) ..... *Apterodromia* (in part)

—— Fore femur slender, lacking long basal setae (Chile) ..... *Neotrichina*

5 Eyes with ommatrichia (New Zealand) ..... *Abocciputa*

—— Eyes bare 6

6 Abdominal sclerites heavily sclerotized, punctate; legs with long slender setae, 2–3 times width of leg segment (Australasian, Neotropical, Oriental, and Palaearctic Regions) ..... undescribed genus B[2]

—— Abdominal sclerites not heavily sclerotized, surface smooth; chaetotaxy of legs variable 7

7 Vein Rs short, arising near apex of cell bm 8

—— Vein Rs long, arising near middle of cell bm 9

8 Hind tibia with at least one large anterior spur; hind femur banded; epandrium usually with row of spines on inner right margin; hind tibia not geniculate at base (Australasia, Chile) ..... *Hoplopeza*[3]

—— Hind tibia with stout bristle, spur usually short and reduced; hind femur not banded; epandrium lacking row of spines on inner right margin; hind tibia generally geniculate at base (Australia, Chile) ..... *Scelolabes*[4]

9 Short M_1 vein arising from cell dm (Australia) ..... *Leptodromia*

—— M_1 vein absent 10

10 Anal lobe not developed, wing narrow; in doubtful cases antennal inserted high on head 11

—— Anal lobe partially or strongly developed, wing broad; antennae inserted near middle of head 12

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1 Key to the major lineages of Australian Empidoidea, including the Ocydromiini, follows this key.

2 This group may contain more than one genus and also includes the Palaearctic species *Leptopeza rugosiventris* Strobl (1910).

3 Also includes *Hoplopeza tachydromiaeformis* (Bezzi, 1904) **n.comb.** from eastern Australia (NSW). It is difficult to assign this species with full confidence because the description does not include an illustration of the wing and the type material is destroyed.

4 The generic separation of *Hoplopeza* and *Scelolabes* remains problematic. Revision of the genera comprising species from all regions is required, including details of female terminalia.

11 Acrostichal setulae present (Australasian, Neotropical, and Palaearctic Regions) ..... *Oropezella*

—— Acrostichal setulae absent (Malaysia) ..... *Stylocydromia*[1]

12 First flagellomere oval; cell cu*p* long, reaching near apex of cell bm (Afrotropical, Oriental, and Holarctic Regions) ..... *Ocydromia*

—— First flagellomere conical; cell cu*p* short, reaching only middle of cell bm 13

13 Hind femur swollen (New Zealand) ..... *Pseudoscelolabes*

—— Hind femur slender (Australia and New Zealand) ..... *Austropeza*

Key to major lineages of Australian Empidoidea

The key to Subfamilies of the Empidoidea presented in the Insects of Australia (Colless & D.K. McAlpine, 1991: 760) lacks several major groups. An updated key (modified from Steyskal & Knutson (1981) and Bickel (1996)) to major lineages and unplaced genera (see Sinclair, 1999) is provided below to assist researchers in sorting and identification of Australian Empidoidea.

1 Wings present 2

—— Wings absent (Ocydromiini) ..... *Apterodromia* (in part)

2 Rs originating at or near level of crossvein h; crossvein r-m in basal fourth of wing; male terminalia rotated forward beneath preceding segments 18

—— Rs originating well distal to level of crossvein h; crossvein r-m distal to basal fourth of wing; male terminalia not rotated forward beneath preceding segments 3

3 Cell dm absent, neither R_{4+5} nor M forked; all veins running without branching to wing margin; cell cu*p* usually lacking, but when present shorter than cells bm and br, and A_1 weak and faint ..... Tachydromiinae

—— Cell dm present or absent; when this cell absent, R_{4+5} or M or both forked, or R_{1+2} forked, or cell cu*p* slender, slightly shorter than cell bm, or foreleg raptorial, or hind first tarsomere with ventral spine-like setae 4

4 Foreleg raptorial, located near head, and distant from others; fore coxa greatly lengthened, at least twice as long as other coxae; fore femur distinctly thickened with at least one row of spine-like setae beneath, never with pair of long, basal spines on short tubercles ..... Hemerodromiinae

—— Foreleg not raptorial; fore coxa short, usually not twice length of other coxae; fore femur not greatly swollen; if leg appearing raptorial, then fore femur with pair of stout basal spines on short tubercles 5

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1 Saigusa (1986) distinguished *Stylocydromia* from other Ocydromiini genera primarily on the basis of the greatly lengthened first flagellomere and the lack of acrostichals. However, certain species of *Oropezella* possess a similarly modified first flagellomere (see Plant, 1989), suggesting that the generic status of *Stylocydromia* may have to be reevaluated. Although known only from just north of the Equator, *Stylocydromia* is likely to be found much further south.

5 Cell cu*p* absent; first flagellomere very large with pedicel inserted thumb-like on inner side at base; proboscis long and slender, arising from front of mouth-opening and slightly recurved ..... Ceratomerinae

—— Cell cu*p* present; first flagellomere normal in size, pedicel without thumb-like extension on inner side; mouthparts variable 6

6 CuA_2 strongly recurved into A_1; in doubtful cases, R_{4+5} branched, or setae present on laterotergite; fore tibia gland lacking 7

—— CuA_2 forming distinct angle with A_1; R_{4+5} unbranched; setae lacking on laterotergite; fore tibial gland present on inner basal margin 17

7 Costa with short, stout or fine erect setae on outer margin or dorsal face; anal lobe of wing not or only weakly developed, forming a broad obtuse angle; labellum sucker-like ..... Clinocerinae

—— Costa without erect setae, if present (*Heterophlebus*) radial veins with setae; anal lobe well developed, usually forming an acute angle; labellum not sucker-like 8

8 Laterotergite with group of setae; R_1 not swollen before joining costa 9

—— Laterotergite bare, if setose then R_1 distinctly swollen before joining costa 10

9 Radial veins setose, with setae on at least dorsal surface of R_1 and ventral surface of R_{2+3}; costa circumambient; female abdomen truncate, terminalia with acanthophorites (Trichopezinae) ..... *Heterophlebus* Philippi

—— Radial veins lacking setae; costa usually ending at or slightly beyond R_{4+5}; female abdomen pointed, terminalia with projecting cerci and no acanthophorites ..... Empidini s.l.

10 Labrum stout, curved posteriorly; fore coxa with numerous erect, spine-like setae; wing narrow with anal lobe weakly developed, forming a broad obtuse angle (*Ragas* group) ..... *Hydropeza* Sinclair

—— Labrum slender or stout, not curved posteriorly; fore coxa lacking erect, spine-like setae; anal lobe of wing usually well developed, forming an acute angle 11

11 CuA_2 little reflexed, apex of cell cu*p* truncate 12

—— CuA_2 strongly reflexed; apex of cell cu*p* rounded 13

12 First flagellomere broadly ovate with short thick stylus (*Ragas* group) ..... *Hormopeza* Zetterstedt

—— First flagellomere elongate, strap-like (known only from Tasmania) (possibly *Ragas* group) ..... new genus 1

13 R_1 distinctly swollen before joining costa; palpus arched forward beneath head; male with basitarsus of foreleg often enlarged or swollen; male terminalia with hypandrium keel-like, forming narrow hood over phallus along posterior margin ..... Hilarini

—— R_1 not swollen before joining costa; palpus straight, projecting obliquely or parallel to proboscis; male with basitarsus of foreleg not swollen; male terminalia with broad hypandrium 14

14 Subcosta complete or practically reaching costa (weakened at extreme apex); male eyes meeting above antennae (holoptic) with upper facets enlarged 15

—— Subcosta distinctly incomplete, fading out well short of costa; male eyes widely separated above antennae (dichoptic) without upper facets enlarged 16

15 Proboscis short or long, if long projecting downwards; male terminalia held near horizontally; female abdomen truncate, terminalia with upright cerci and acanthophorites (Trichopezinae) ..... *Apalocnemis* Philippi

—— Proboscis long and slender, projecting obliquely forward; male terminalia held upright, almost vertically; female abdomen pointed, terminalia with cerci projecting horizontally and no acanthophorites (often collected on blossoms) (*Iteaphila* group) ..... new genus 2

16 First flagellomere strap-like, elongate and thickened; apical flagellomeres style-like, shorter than first flagellomere (commonly found on rocks in streams and rivers) (probably Trichopezinae) ..... new genus 3

—— First flagellomere short, pointed ovate; apical flagellomeres arista-like, longer than first flagellomere (known only from Tasmania) (*incertae sedis*) ..... new genus 4

17 Cell cu*p* usually truncate, shorter than cell bm; if longer hind legs slender, not raptorial; eyes not meeting above antennae (dichoptic) in females and without upper facets enlarged ..... Ocydromiini

—— Cell cu*p* as long as or longer than cell bm, with apex arched to meet A_1 at acute angle; eyes meeting above antennae (holoptic) in both sexes with upper facets enlarged ..... Hybotinae

18 Cell dm closed, crossvein bm-cu complete or nearly so; M forked, both branches reaching wing margin; costa circumambient; body generally black ..... Microphorinae

—— Cells dm and bm confluent, crossvein bm-cu absent or distinctly abbreviated; if M forked then M_2 not reaching wing margin; costa ending at R_{4+5} or M_1; body generally yellow or green metallic ..... Dolichopodidae

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Native Earthworms (Oligochaeta) from Southeastern Australia, with the Description of Fifteen New Species

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ABSTRACT. This paper describes 15 new and five known endemic earthworm species, and provides keys to New South Wales genera. Two new species of *Plutellus* require expansion of the generic diagnosis to allow species with short stalks to the calciferous glands (always subordinate to the plesiomorphic tubular prostates that characterise this genus and distinguish it from *Heteroporodrilus*). For *Vesiculodrilus*, the nominal type species of the genus, *V. frenchi* (Spencer, 1892), is redescribed and figured on a neotype. Nephridial vesicles, essential for inclusion in *Vesiculodrilus*, are newly reported in *V. frenchi*. Two new species from Mt Kosciuszko are added to this genus.

Syntypes of *Heteroporodrilus canaliculatus* (Fletcher, 1889) and *H. mediterreus* (Fletcher, 1887b) are rediscovered, lectotypes are designated, and these species are redescribed. Six new species are added to *Heteroporodrilus* requiring the generic diagnosis to be amended to accept calciferous glands that are stalked, sessile, or annular. Intermittent nephropore alternation to mid-setal lines, once thought diagnostic only of *H. shephardi* (Spencer, 1900), is reported in several other species. The close affinities amongst heteroporodrilids widely distributed in New South Wales, Queensland, Victoria and South Australia is accounted for by fluvial transport along the river systems such as the Murray-Darling.

New material of *Cryptodrilus fastigatus* Fletcher, 1889 is described and a congeneric species proposed, allowing explanation of the intraspecific variation in their male fields: The pore-like "genital markings" are actually modified nephropores that function for excretion, rather than copulation. One species of *Megascolides* from Bago-Maragle State Forest is newly described; variation in forms of tubular prostates is briefly considered in remarks following this species' description. Two new species are added to *Notoscolex*, and one new species to *Digaster*.

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Australian native earthworms belong to the Acanthodrilidae, a relatively primitive family now predominantly confined to the northerly regions (Blakemore, 1997b), and the Megascolecidae which is both more derived and more widespread. This paper considers various megascolecid genera from the southeastern states, especially New South Wales, complementing a paper (Blakemore, 2000) that dealt only with the genus *Anisochaeta*. The methodology employed in both these studies is similar as much of the material examined was from Easton's 1983 NSW Collection at the Australian Museum, Sydney. Many unidentified specimens in this collection were found to be new species

requiring description. The opportunity was also had to inspect type material of described taxa of earlier workers that are housed in the Australian Museum. Additional material was mainly from specimen identification requests to the author relating to ecological, agronomic or conservation studies.

There are various systems of higher level classification currently in use, those that are most widely accepted owe much to the "classical system" (as defined by Gates, 1959: 235), devised by Michaelsen (1900) as adopted by Stephenson (1930) and extended by Sims (1982) (see Lee, 1994). In the current paper the arrangement of genera largely follows Michaelsen (1907), updated for the most current taxonomic nomenclature, in which the plesiomorphic character states are tubular prostates, holoic nephridia, and lumbricine setae. Any derivation from these basic states are considered apomorphies. Characters of the digestive system (position and development of gizzard, calciferous glands and intestine) are of secondary taxonomic importance. Australian native species characteristically have one or more oesophageal gizzards in or near segment 5.

The following key to native earthworm genera in NSW is only preliminary, pending revision of genera from other Australian states and from New Zealand (currently in preparation by the author). Information and lists of exotic species known from Australia are presented by Blakemore (1999).

Preliminary key to native earthworm genera of New South Wales

1 Pores from two pairs of tubular prostates on 17 and 19 (or one pair on 17) separate from male pores on 18 (or on 17): Acanthodrilidae ..... *Diplotrema*

—— Pores from tubular to racemose prostates combined with male pores on 18: Megascolecidae 2

2 Prostates tubular (i.e., glandular part elongate with simple unbranched canal) 3

—— Prostates tubuloracemose (i.e., elongate but with incised surface and central canal receiving canalicules) or racemose (i.e., lobular with branching or ramifying canal system) 9

3 Holoic (i.e., nephridia one pair per segment, excluding pharyngeal tufts) 4

—— Meroic (i.e., nephridia more than one pair, at least in fore-body) ..... *Megascolides*

4 Lumbricine (i.e., 8 setae per segment) 5

—— Perichaetine (more than 8 setae, at least in mid- or hind-body) ..... *Diporochaeta*

5 Nephridia absent from anterior until c. segment 13 (littoral) ..... *Pontodrilus*

—— Nephridia present from anterior (terrestrial or semi-aquatic) 6

6 Male pores (and spermathecal pores) paired 7

—— Male pores and spermathecal pores unpaired ..... *Fletcherodrilus*

7 Nephridia vesiculate (i.e., with ducts dilated to form terminal bladders) 8

—— Nephridia avesiculate ..... *Graliophilus* (mostly inWA?), *Simsia* (Vic.), or *Hiatidrilus/Sebastianus* (mostly in Qld)—these genera require resolution.

8 Nephridia exiting with regular alternation in *d* to *b* lines ..... *Plutellus*

—— Nephridia without regular alternation ..... *Vesiculodrilus*

9 Holoic (i.e., nephridia one pair per segment, excluding pharyngeal tufts) 10

—— Meroic (i.e., nephridia more than one pair, at least in fore-body) 13

10 Lumbricine (i.e., 8 setae per segment) 11

—— Perichaetine (more than 8 setae, at least in mid- or hind-body) 12

11 Nephridia avesiculate ..... *Zacharius* (NSW) or *Woodwardiella* (in WA, Vic.).

—— Nephridia vesiculate with regular alternation in *d* to *b* lines ..... *Heteroporodrilus*

12 Gizzard well developed (in segment 5) ..... *Perionychella* or *Terriswalkerius* (in Qld).

—— Gizzard rudimentary ..... *Perionyx* (not native to Australia).

13 Lumbricine (i.e., 8 setae per segment) 14

—— Perichaetine (i.e., more than 8 setae, at least in mid- or hind-body) 18

14 Gizzard single (in, or adjacent to, segment 5) 15

—— Gizzards in two or three segments (between 4–7) 16

15 Nephridia avesiculate ..... *Notoscolex*

—— Nephridia vesiculate ..... *Cryptodrilus*

16 Two or three gizzards, dorsal pores present 17

—— Three gizzards, dorsal pores absent ..... *Perissogaster*

17 Spermathecal pores (two pairs) intersegmental ..... *Digaster*

—— Spermathecal pores (three pairs) segmental ..... *Didymogaster*

18 Gizzard in segment 5 (or adjacent) ..... *Anisochaeta*

—— Gizzard in segment 8 ..... non-native pheretimoids (see Blakemore, 1999).

Methodology and abbreviations

Methods and terminology are similar to those in Blakemore (2000). Segments are counted from the anterior in Arabic numerals (female pores are on 14 and male pores on 18 in megascolecids, unless counts are reduced by suppression of anterior segments); intersegments are designated by a slash (e.g., 1/2); variations are shown by a comma and range by a dash (e.g., 3,4–5). Setae, counted from the ventral-most on each side, have lower case letters (e.g., *a b c d*); variations are shown by a comma and range by a dash (e.g., *a,b-c*); setal lines refer to longitudinal setal series. In lumbricine species, the relative position of the four setae on one side of segment 12 are figured. Dissection is by dorsal incision longitudinally, the specimen being pinned on a wax tray while immersed in ethanol. While most features and anatomical details are symmetrical, where these differ on one side to the other the description always refers to the observers point of view (lhs—left hand side; rhs—right hand side). The clitellum is shaded and other structures of taxonomic significance are shown in the figures (these are labelled in Fig. 1). All specimens were sketched in the author's usual style using a camera lucida, and all scale bars are 1 mm.

Notes on distribution and habitat follow each species' description—these are intended (along with the morphology and gut contents) to give some indication of ecological strategy and species associations, as well as to assist fieldworkers locate further material.

Abbreviations: AM—Australian Museum, Sydney; ANIC—Australian National Insect Collection (CSIRO Entomology, Canberra); NMV and MOV—formerly National Museum of Victoria, now Museum of Victoria, Melbourne; SAM—South Australian Museum, Adelaide. H refers to holotype, N to neotype, P to paratypes and S to specimens.

Systematics results

Genus *Plutellus* Perrier

Plutellus Perrier, 1873: 250; Michaelsen, 1900: 163, 1907: 159; Stephenson, 1930: 833; Jamieson & Nash, 1976: 45; Dyne, 1981: 96; Blakemore, 1994b: 35.

Diagnosis. Setae lumbricine (i.e., eight per segment). Male pores on 18 combined with pores of tubular prostates. Gizzard well developed in 5; four pairs of extramural calciferous glands present in 10–13 on long, or (*P. buckerfieldi*) short, stalks. Nephridia vesiculate holoic (i.e., one pair per segment with terminal dilations of the ducts forming large bladders); nephropores in anterior in setal *d* or *c* lines then, after segments 5–7, alternating regularly from *d* to *b* lines. Spermathecae five or fewer pairs with single, uniloculate diverticulum.

Type species. *Plutellus heteroporus* Perrier, 1873, from Port Macquarie and Barrington Tops, central NSW. (Types in the Muséum national d'Histoire naturelle, Paris).

Included species

Plutellus barringtoni n.sp. from Barrington Tops, NSW.
Plutellus buckerfieldi n.sp. from Namoi Rv., Gunnedah, NSW.
Plutellus heteroporus Perrier, 1873, from Port Macquarie and Barrington Tops, central NSW.
Plutellus hutchingsae Jamieson, 1977 from Lord Howe Island.
Plutellus manifestus (Fletcher, 1889: 1538) from Waterfall, Royal National Park, and Bulli, in southern coastal NSW. (Syntypes, AM W1371).

Species inquirendum

Plutellus rubens (Fletcher, 1887a: 381) from Mt Wilson, Blue Mountains, NSW.

Distribution. Central and southern coastal New South Wales, (Lord Howe Island). Perrier supposed his type series was from Pennsylvania, but the locality is now known to be Australian in coastal New South Wales, in the vicinity of Port Macquarie (Gates, 1972: 38; Blakemore, 1994b: 35–37; see also Distribution and habitat under *P. barringtoni* below).

North American species of *Plutellus* were transferred to *Argilophilus* (as mooted by Gates, 1972: 38) and to other genera by Fender & McKey-Fender (1990).

Remarks. The most recent revision of this genus is by Blakemore (1994b); see also remarks after *Heteroporodrilus* below.

Key to the known species of *Plutellus*

1 Spermathecae five pairs 2

—— Spermathecae four pairs 3

2 Spermathecae five pairs in setal *b* lines ..... *Plutellus heteroporus*

—— Spermathecae five pairs in setal *a* lines ..... *Plutellus hutchingsae*

3 Last hearts in 13; penial setae present; calciferous glands on short stalks ..... *P. buckerfieldi* n.sp.

—— Last hearts in 12; penial setae absent; calciferous glands on long stalks 4

4 Spermathecal pores mid-ventral ..... *P. manifestus*

—— Spermathecal pores lateral of setal *a* lines ..... *P. barringtoni* n.sp.

Plutellus barringtoni n.sp.

Figs. 1, 20

Material examined. HOLOTYPE: AM W24409 (H), Barrington Tops, c. 31°59'S 151°30'E, Ed Easton, 16.iii.1983; labelled, "Jar 12 Sp 55", "AM No 12 *Diporochaeta* gp., ♀ [spermathecae symbol] ×3 or 4, Barrington Tops Trail. Colourless", (complete mature, figured and dissected). PARATYPES: ANIC RB.98.2.4, (P1), same details as H, (aclitellate mature, damaged in mid-body, dissected); AM W24411, (P2), same details as H, (subadult, dissected); ANIC RB.98.2.5, (P3), same details as H, (subadult).

External features. Body almost triangular in section posteriorly with *b-b* flat, dorsum not canaliculate. Lengths mm: 80 (H), 60–74 (Ps). Width: c. 2–3 mm. Segments: 158

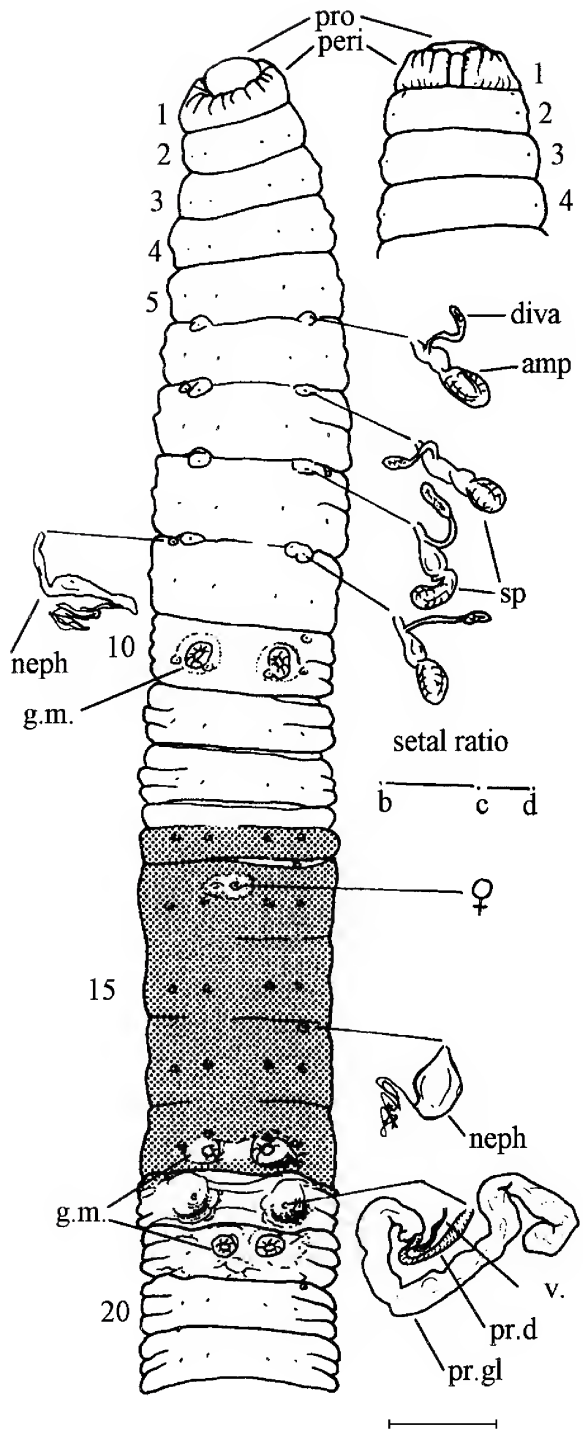

Figure 1. *Plutellus barringtoni* n.sp., ventral view of holotype with dorsal view of prostomium; spermathecae *in situ*; nephridial bladders in segments 9 lhs, 16 rhs; tubular prostates and vasa deferentia in 18 (penial setae are absent). Abbreviations: amp—spermathecal ampulla; diva—spermathecal diverticulum; g.m.—genital marking; neph—nephridium (to nephropore); peri—peristomium; pro—prostomium; sp—spermatheca (opens to spermathecal pore); pr. d.—prostatic duct (opens to male pore); pr.g.—prostatic gland; v.—vasa deferentia. Scale 1 mm.

(H), range 147–196 (Ps). Colour: unpigmented, mid-body almost translucent, clitellum russet. Prostomium: narrowly tanylobous. Clitellum: ½13–½18 (pale ventrally in ½17–½18). Dorsal pores: possibly in 10/11 but not definite till 13/14, as white dots on clitellum and small afterwards (H); from 7/8 (P1–3). Setae: small 8 per segment in regular rows. Nephropores: at anterior margin of segment in *d* lines in 2, 7 (rhs) then with regular alternation; in *c* lines in 3–6; in *b* lines 7 (lhs) then with regular alternation (H). Spermathecal pores: on small papillae in 5/6/7/8/9 in *ab* lines but closer to setal *a* lines. Female pores: paired on 14. Male pores: paired on wide mounds in *ab* lines on 18. Genital markings: paired, presetal sucker-like discs in *ab* lines on 10 (H) or 10 and 11 (P1–3); more ventrally paired in 17 and 19 but postsetal and presetal, respectively; (plus in P1 only) smaller paired postsetal discs median of *aa* in 19 and 20.

Internal anatomy. Septa: 5/6–10/12 slightly thickened. Gizzard: large muscular barrel in 5. Oesophagus: paired reniform calciferous glands ventrolateral on long stalks in 10–13 (i.e., four pairs); valval in 14. Nephridia: vesiculate holoic, bladders elongate in anterior, more sub-spherical in posterior, position alternating with nephropores. Vascularization: large dorsal blood vessel single onto gizzard; hearts paired in 10–12; weak supra-oesophageal vessel seen in 11–13 only. Spermathecae: four pairs in 6–9, bulb-like ampulla on equally long thick duct, narrow long-stalked ectal diverticulum with dilated terminal bulb (inseminated). Male organs: holandric, iridescent testes and funnels in 10 and 11; seminal vesicles small paired in 9 and 12. Ovaries: compact in 13; small ovisacs in 14. Prostates: tubular in 18–19, duct slight (H) to strongly dilated (P1), vasa deferentia join at junction of gland and duct; penial setae not found. Intestine: origin 15; no typhlosole; gut contains fine yellow soil.

Remarks. Although there is slight variation in position of dorsal pores and genital markings in the paratypes, all specimens are regarded as conspecific as the dissected specimens agree internally. *Plutellus barringtoni* has four pairs of spermathecae in segments 6–9 as have *P. manifestus* and *P. buckerfieldi*. In *P. manifestus* however, the spermathecal pores are mid-ventral and remarkably close together; *b* setae converge on either side of the male pores and the distribution of genital markings differs. Differences from *P. buckerfieldi* are given in the description of this species below. The major differences from *P. heteroporus* are four, rather than five, pairs of spermathecal pores that are closer to setal *a* lines, rather than setal *b* lines, and longer spermathecal diverticula.

Etymology. Named after the type locality.

Distribution and habitat. Barrington Tops National Park is an elevated, forested plateau north of the Hunter River and c. 150 km inland from the Port Macquarie type-locality of *Plutellus heteroporus*. In the current study, specimens of *P. heteroporus* (viz. AM W24416–24417, ANIC RB.98.2.9–10) were found sympatrically with *P. barringtoni* in material collected by Ed Easton from Junction Holes, Barrington Tops. Also found in the Easton collection from the vicinity

of Barrington Tops were an unidentifiable, damaged plutelloid (W24418); *Anisochaeta erica* and *A. palustris*, both described by Blakemore (2000); several other *Anisochaeta* spp. that are currently undescribed; plus a specimen (W20775) labelled "Moniligastridae" that is actually a tubificid (pers. obs.).

Plutellus buckerfieldi n.sp.

Figs. 2, 20

Material examined. HOLOTYPE: ANIC RB.97.3.3 (H), from clay riverbanks of Namoi River, near Gunnedah, central NSW, specimen donated by J.C. Buckerfield, labelled "Coll: Brian Dawson ('Active Earthworms'), Grovers Lane, Glen Innes, NSW 2370, 22.iv.1994", (complete mature, figured and dissected). PARATYPES: none.

External features. Body faintly dorsally canaliculate throughout. Length: 170 mm. Width: c. 6 mm. Segments: 203. Colour: body grey, dorsum to *c* lines darker slate; clitellum puce. Prostomium: tanylobous, dorsally furrowed. Clitellum: weak ¼13–17. Dorsal pores: vestigial in 6/7, open from 7/8. Setae: 8 in regular series. Nephropores: at anterior margin of segments in *d* lines in 2–4; ventral of *c* lines in 5 and 6 (rhs); in *b* lines with regular alternation from 6 (lhs) or 7 (rhs) and in *d* lines from 7 (lhs) or 8 (rhs); but by final third of body alternations become symmetrically aligned in each segment. Spermathecal pores: small in 5/6/7/8/9 in setal *a* lines. Female pores: paired just anteromedian to setae *a* on 14. Male pores: aligned with setal *a* lines on small papillae on 18. Genital markings: paired, presetal in line with spermathecal pores in 9–12; paired, postsetal in *ab* lines in 17 and paired presetal in *ab* lines in 19; both sets of posterior markings converge towards the male pores.

Internal anatomy. Septa: 9/10–12/13 slightly thickened. Gizzard: in 5 muscular tapering barrel. Oesophagus: paired reniform calciferous glands ventrolateral on short ducts, almost sessile in 10–13 (i.e., four pairs); valvular in 14–½15. Nephridia: vesiculate holoic with bladders elongate in anterior and ocarina-shaped in posterior, alternating in position with nephropores. Vascularization: dorsal blood vessel single; hearts paired in 10–13; supra-oesophageal vessel seen in 10–13 with connectives to hearts and calciferous glands. Spermathecae: four pairs in 6–9, tapering ampulla on almost equally thick duct with long stalked ectal diverticulum having dilated terminal bulb (iridescent). Male organs: holandric, iridescent testes and funnels in 10 and 11 invested in mucus; seminal vesicles paired, racemose in 9 and 12, latter pair with many small nodules. Ovaries: fan-shaped composed of numerous minute egg-strings in 13; no ovisacs found in 14. Prostates: tubular in 18–19, vasa deferentia attach at junction of gland and thickened duct; long and fine penial setae overlie duct. Intestine: from ½15, especially dilated to 17; no typhlosole; gut contains gritty organic soil and plant remains.

Remarks. *Plutellus buckerfieldi* differs from other known members of the genus in the reduced stalks to the extramural calciferous glands (requiring the introduction of this characterization, always subsidiary to tubular prostates, in the generic diagnosis above). *Plutellus buckerfieldi* has four pairs of spermathecae and four pairs of calciferous glands, as have *P. manifestus* and *P. barringtoni*. However, in these latter two species the last hearts are in 12, they lack penial setae and dorsal canaliculation, and the genital markings differ. There is a gradation in position of spermathecal pores: midventral in *P. manifestus*, in setal *a* lines in *P. buckerfieldi*, lateral of *a* lines in *P. barringtoni*, and (with an extra pair in 4/5) in *b* lines in *P. heteroporus*. The male pores of these species diverge correspondingly.

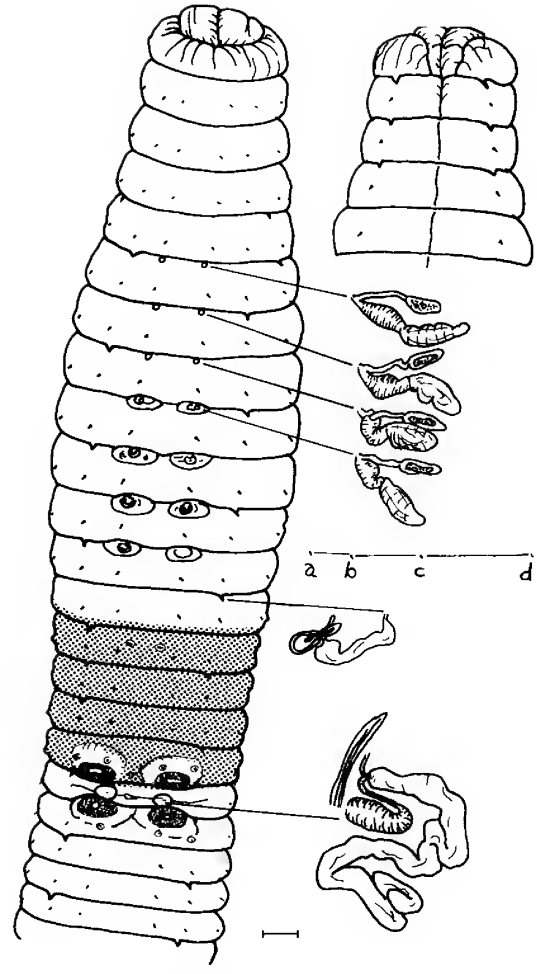

Figure 2. *Plutellus buckerfieldi* n.sp., ventral view of holotype with dorsal view of canaliculate prostomium; spermathecae; nephridial bladder in 13 rhs; tubular prostate and penial setae in 18. Scale 1 mm.

Etymology. Named after John Buckerfield of Adelaide.

Distribution and habitat. Gunnedah, on the banks of the Namoi River, is about 250km inland from the NSW central coast. Introduction of these worms, collected at Gunnedah, into paddocks on clay soils of a property in Glen Innes was made in an attempt to improve soil structure and pasture production (B. Dawson, pers. comm., 7 October 1998). It is not known whether the introduced specimens survived.

Genus *Vesiculodrilus* Jamieson

Vesiculodrilus Jamieson, 1973: 224.
Perionychella (Vesiculodrilus) Jamieson, 1974a: 216.
Pinguidrilus Jamieson, 1974a: 263, **new synonym**.

Diagnosis. Setae lumbricine. Male pores on 18 combined with pores of tubular prostates. Gizzard in 5; extramural calciferous glands absent (rudimentary annular glands may be present); typhlosole absent. Nephridia vesiculate holoic (i.e., one pair of tubules per segment with terminal dilations of the ducts forming large bladders); nephropores in a single row on each side near *c* lines or sinuous in *c* lines and above. Spermathecae five or fewer pairs each with single, uniloculate diverticulum. Penial setae present or absent.

Type species. *Cryptodrilus frenchi* Spencer, 1892 from Croajingolong, Victoria. (NEOTYPE, newly designated: AM W1289).

There is some confusion with the type species of this genus. Jamieson (1973) considered the NSW specimens, on which he based the genus, to agree with *C. frenchi* Spencer. However, comparison of these NSW specimens with the neotype of *C. frenchi* as described below demonstrates that they are not conspecific. Nevertheless, the neotype of *C. frenchi* happens to agree with the genus as defined, in particular by having vesiculate nephridia (previously unmentioned by Spencer). The type species is herein fixed (under Article 70.3 of the Code, ICZN, 1999) as *Cryptodrilus frenchi* Spencer, 1892 misidentified with *Vesiculodrilus nivalis* n.sp. in the original designation by Jamieson (1973).

Included species. Three NSW species, all from Mt. Kosciuszko region, are *Vesiculodrilus nivalis* n.sp., *Vesiculodrilus purpureus* Jamieson, 1973 [probably a junior synonym of *V. victoriae* (Spencer, 1892)], and *Vesiculodrilus vallis* n.sp. Of the Victorian species included in *Vesiculodrilus* by Jamieson (1973: 225), *Megascolides tisdalli* and *M. volvens*, both of Spencer, 1900, have setae reputedly increasing beyond 8 per segment (i.e., perichaetine) which would place them in *Diporochaeta* Beddard, 1890. Similarly, several perichaetine species from Tasmania, Victoria and Queensland listed under *Perionychella (Vesiculodrilus)* by Jamieson (1974a: 222) are excluded from *Vesiculodrilus* as defined above. Complete lists of species are currently precluded by lack of information on nephridial states from some earlier descriptions. Checking of Victorian species with five or fewer pairs of spermathecae for presence or absence of nephridial bladders is beyond the scope of the present work; however, studies by the author have identified 10 known and approximately 50 new species of *Vesiculodrilus* from Tasmania that comply with the diagnosis above (Blakemore, in prep.).

Distribution. Tasmania, Victoria, southern New South Wales.

Remarks. Retained as a subgenus of *Perionychella* Michaelsen, 1907 by Jamieson (1974a) and reassigned to *Diporochaeta* by Jamieson (1976), *Vesiculodrilus* is herein restored to its original generic rank in recognition of its morphological distinctness. The generic definition is expanded: Firstly, to accept species with nephropores in irregular series as found in *Vesiculodrilus tasmanianus* (Fletcher, 1887b) following the present author's discovery of spermathecal diverticula in the Museum of Victoria lectotype (Blakemore, in prep.)—thereby removing justification for the monotypic genus *Pinguidrilus* Jamieson, 1974a. Secondly, to accept species with fewer than the five pairs of spermathecae diagnosed by Jamieson (1973). Several Tasmanian species have fewer than five pairs of spermathecae, but the nephridial states of such species from Victoria have yet to be determined.

Characteristics of holonephry, lumbricine setae and tubular prostates are all plesiomorphic states shared with *Graliophilus* Jamieson, 1971, its possible junior synonym *Hiatidrilus* Jamieson, 1994, and with *Sebastianus* Blakemore, 1997b, indicating the relatively primitive nature of these genera. However, the type species of these latter three genera lack nephridial vesicles whereas these structures invariably occur in *Vesiculodrilus*. Possibly this character is apomorphic in *Vesiculodrilus*, although the vesiculate state is found in the more primitive family Acanthodrilidae in some species endemic outside Australia. Related genera in the eastern subregion of mainland Australia are *Plutellus* which, unlike *Vesiculodrilus*, has regular alternation of nephropores and extramural calciferous glands, and *Fletcherodrilus* Michaelsen, 1891 that typically has unpaired male and spermathecal pores. Species with holonephridia (with or without bladders) but attaining greater than eight setae (the perichaetine condition) are assignable to *Diporochaeta* s.str. if they have tubular prostates, or to *Perionychella* s.str. if their prostates are other than tubular (i.e., tubuloracemose or racemose). (A recently proposed Queensland genus, *Terriswalkerius* Jamieson, 1994, on the justification presented, appears to subsume the characteristics of either of these two prior genera, and therefore its included species should probably be reallocated to *Diporochaeta* or *Perionychella* depending on whether they have tubular or non-tubular prostates, respectively).

Vesiculodrilus frenchi (Spencer, 1892)

Fig. 3a,b

Cryptodrilus frenchi Spencer, 1892: 135–136, figs. 10–12, 66.
Megascolides frenchi.–Beddard, 1895: 493.
Plutellus frenchi.–Michaelsen, 1900: 175.
Non *Vesiculodrilus frenchi* sensu Jamieson, 1973: 225–227, fig. 2A; non *Cryptodrilus frenchi* Spencer, 1892a *sensu* Jamieson, 1974a: 221–222; non *Vesiculodrilus frenchi* (Spencer) sensu Jamieson, 1974a: 222; non *Perionychella (Vesiculodrilus) frenchi* sensu Jamieson, 1974a: 221–222.

The specimens described by Jamieson (1973) do not agree sufficiently with Spencer's species to be considered conspecific (see *Vesiculodrilus nivalis* n.sp. below). In his synonymy, Jamieson (1973) has also confused *Cryptodrilus frenchi* Spencer, 1892 with *Perichaeta frenchii* Spencer, 1893.

Material examined. NEOTYPE: AM W1289 (N), part of the Fletcher Collection presented to the Australian Museum; the sample jar contained a metal tag "W1289" plus three

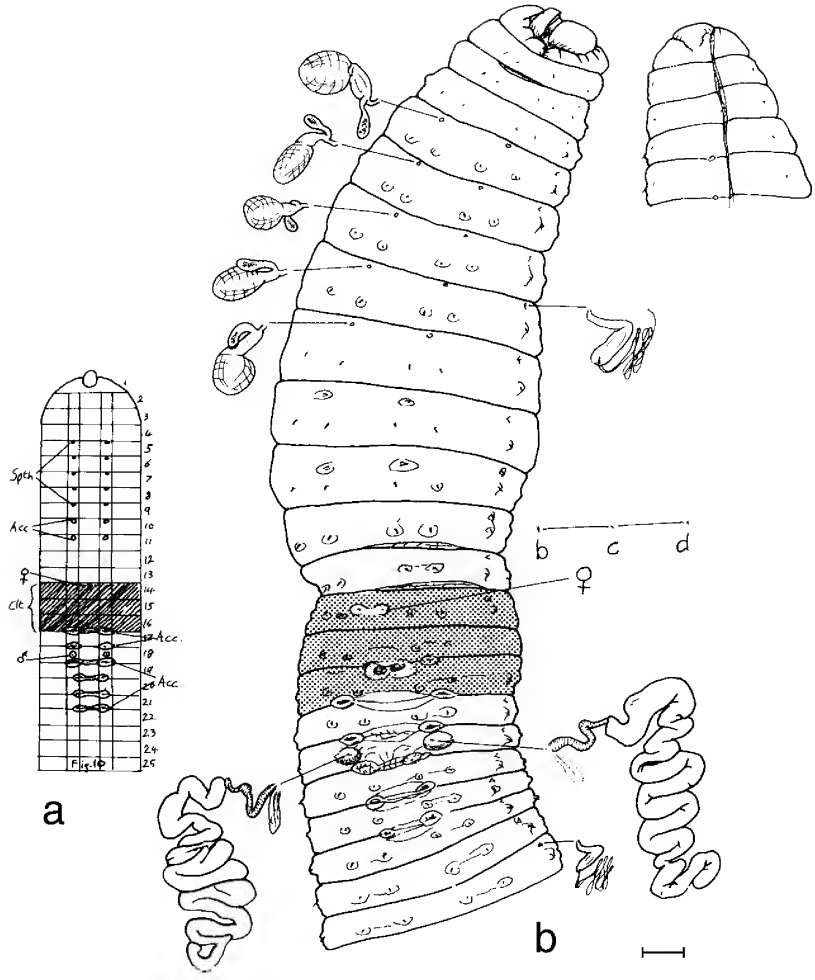

Figure 3. a, *Vesiculodrilus frenchi* (Spencer, 1892), after Spencer's original figure 10; b, *Vesiculodrilus frenchi* (Spencer, 1892) ventral view of neotype with dorsal view of sectioned prostomium, spermathecae *in situ*; nephridial bladders in 8 rhs and 23 rhs; both sets of prostates in 18–21, 22 with penial setae remaining only on lhs. Scale 1 mm.

labels: "*Plutellus frenchi* (Sp.)" [in pencil in Fletcher's hand?]; "W1289 *Plutellus frenchi* / Croajingolong, VICTORIA / Pres: J.J. Fletcher"; "AM W1289 *Diporochaeta frenchi* / Locality: Croajingolong, Vic. / Pres: J.J. Fletcher / Id: by E. Easton, '83". Two specimens were originally present, plus a middle fragment of a third specimen. The previously dissected, complete mature specimen with metal stud in tail (part of metal tag?) described and figured here is designated the neotype (N); the other specimen, AM27081 (ex W1289) a complete mature specimen, also previously dissected, is designated specimen (S1) (see Remarks below).

External features (compared with Spencer's type description). Body circular in section, fairly stout. Lengths mm: 85 (N), 80 (S1) (cf. 75 Spencer). Width: 5–6 mm (cf. c. 4 mm Spencer). Segments: 113 (N), 103 (S1). Colour: uniform light brown in alcohol, clitellum only slightly darker. Prostomium: tapering epilobous; peristomium ventrally cleft. Clitellum: 14–16. Dorsal pores: from 4/5. Setae: 8 in regular rows except final 16 (N) or 30 (S1) segments where all but setal *a* lines irregular. Nephropores: in *c* lines. Spermathecal pores: at anterior of segments near 4/5–8/9 in *ab* just lateral to *a* lines ("just on the very anterior boundaries of segments 5–9, at the level of the interval between the inner couple of setae", Spencer). Female pores: paired on 14. Male pores: at centres of small mounds at interval of *ab* lines on 18. Genital markings: on 10 and 11 (N) (ditto Spencer), or on 11 only (S1), small paired pinched ellipses with pore-like centres at anterior of segments just lateral to setal *a* lines; in 15/16 (N only) a pair of weak markings median to setal *a* lines; in 16/17–20/21 (N), or 16/17–19/20 (S1) (cf. between 16–21,22 Spencer) paired intersegmental markings, in *ab* lines anterior to male pores, in *a* lines posterior to male pores, each conjoined by tumid furrows.

Internal anatomy. Septa: 5/6 thin to base of gizzard, 10/11/12 slightly thickened. Gizzard: compact muscular in 5 but displaced to appear in 6 (removed from S1) (cf. "small in 6", Spencer). Oesophagus: dilated in 12–14 perhaps forming rudimentary annular calciferous glands (cf. "vascular swellings in 9–15, but no true calciferous glands", Spencer). Nephridia: vesiculate holoic, bladders elongate;

pharyngeal tufting not noted. Vascularization: dorsal blood vessel (damaged by dissection, where visible) single; last hearts in 12, supra-oesophageal vessel 8–½13 (ditto Spencer). Spermathecae: five pairs in 5–9 (in both specimens, those from 9 rhs removed and missing from jar), large saccular ampulla on tapering duct with medium-sized diverticulum ectally. Male organs: holandric, iridescent testes and funnels in 10 and 11; seminal vesicles paired large posteriorly in 9, small posteriorly in 10, anteriorly in 12 (cf. in 9 and 12 Spencer). Ovaries: in 13 (only oviducts found); ovisacs not noted. Prostates: tubular 18–21,22; penial setae present (in N, rhs removed). Intestine: damaged by dissection (both N and S1), origin perhaps near 16 (not determined by Spencer); typhlosole absent; gut contains mainly woody organic material.

Remarks. The body cavity of specimen (N) was heavily infected with *Monocystis*. The material examined above agrees with Spencer's original description. The only notable differences are slight variations in the distribution of genital markings, the gizzard in the more normal position in segment 5 rather than in 6, and the presence of small seminal vesicles in segment 10 as well as in 9 and 12 (although only the "finger-shaped" pair in 9 shown in Spencer, fig. 12). Newly recorded here are the presence of nephridial bladders and of penial setae, and the absence of a typhlosole. (In his preliminary notices, Spencer [1892: 130] purposely refrained from recording these structures).

Spencer (1892: 135) was ambiguous regarding the location of the posterior genital markings: "Patches on each side of the body at the level of the interval between the inner couple of setae from segments 16–21. Each patch is composed of a small part of two contiguous segments and the pairs are united across the mid-ventral line by glandular ridges." They may thus be interpreted as occurring between *ab* in 16/17–20/21, although Spencer (fig. 10) shows them in 16/17–21/22 narrowing posteriorly. (Similar ambiguity occurs in the description and figure of his preceding species, *Vesiculodrilus tanjilensis* [Spencer, 1892]).

Jensz & Smith (1969: 87) were unable to locate type specimens in the Spencer Collection at the Museum of Victoria. Documentation is lacking (e.g., no inventory nor labels in Spencer's hand), but the material examined above is probably part of this missing type-series because, apart from their close morphological agreement, the labelling shows they are identified from the type-locality. Moreover, some other missing material has been located during the present study in Spencer's associate Fletcher's donation to the Australian Museum (e.g., *Megascolides diaphanus* Spencer, 1900, see under this genus' Remarks below; see also *Heteroporodrilus shephardi* below). However, as it is not possible to prove indisputably that they are part of the lost type series (i.e., syntypes), and in absence of any other known material, one specimen is here designated the neotype (under Article 75 of the ICZN Code).

Distribution and habitat. Croajingolong National Park is a large coastal reserve in East Gippsland, Victoria, bordering NSW at its northern end. Species described by Spencer (1892, 1893) from the same locality along with *Cryptodrilus frenchi*, were *C. (= Vesiculodrilus?) gippslandicus, Megascolides (= Notoscolex) cameroni, Perichaeta (= Anisochaeta) frosti, P. goonmurk* and, probably, *Cryptodrilus dubius*. For this last species, Jensz & Smith (1969: 87) reiterate Spencer's statement "This probably comes from Croajingolong" but the distinct locality other than Victoria is not noted; they also report that the types of the other species were collected at Croajingolong in January 1889, during an expedition of the Field Naturalists' Club of Victoria.

Vesiculodrilus nivalis n.sp.

Vesiculodrilus frenchi (Spencer, 1892); Jamieson, 1973: 225–227, fig. 2A (misidentification).

Material examined. HOLOTYPE: AM W4693, labelled "*Cryptodrilus frenchi*, Mt Kosciuszko, NSW 36°59'S 148°59'E, 17(140/2), Alpine herbfield... Coll: T.G. Wood, 10 Nov. 1967. Det. B. Jamieson"; and "*Cryptodrilus Frenchi* Spencer, 1892 No. 89 one specimen" [in Wood's hand], tagged "T36" (complete mature, previously dissected, and agreeing externally with Jamieson's fig. 2A [of his Specimen 1?] and mostly agreeing internally with Jamieson's description [of his Specimen 4?], especially in the multi-diverticulate form of one spermatheca). There is some confusion with Jamieson's "Specimen" numbers, descriptions, and registrations. It is deduced that Jamieson's "Specimen 1" and "Specimen 4" are variously the same as the previously dissected specimen, "Specimen 3", herein designated the holotype (H). PARATYPES: AM W4692, from same sample, labelled "*Cryptodrilus Frenchi* Spencer, 1892 No. 87 one specimen" [in Wood's hand], tagged "T34" (complete mature, length = 140 mm, undissected but cuticle removed and cut in mid-body)—probably Jamieson's "Specimen 2", here designated paratype (P1). AM W4691, from same sample, labelled "*Cryptodrilus Frenchi* Spencer, 1892 No. 88 one specimen" [in Wood's hand], tagged "T35" (mature posterior amputee; previously undissected now desiccated and, despite re-immersion in ethanol, of little use)—possibly Jamieson's "Specimen 1", here designated paratype (P2). Additional material—Jamieson's "Specimen 4" from the same site, lodged at CSIRO Department of Soils (= Division of Land and Water), Glen Osmond, Adelaide, not located.

External features from Jamieson (1973) and reinspection of type-series. Body faintly canaliculate dorsally in forebody. Lengths (mm): 120 (H), 140 (P1). Width: c. 5 mm. Segments: 112 (H). Colour: pale; clitellum buff. Prostomium: tanylobous; peristomium ventrally cleft. Clitellum: 14–16. Dorsal pores: minute in 3/4, open from 4/5. Setae: 8 in regular rows except on tail. Nephropores: *c* lines? Spermathecal pores: minute at anterior of segments near 4/5–8/9 in setal *a* lines. Female pores: on 14 near *a* lines. Male pores: equatorial on small mounds in *ab* lines on 18. Genital markings: on 9–11 (H) or 10–11 (P1) small sucker-like discs presetal in *ab* lines; markings in 16/17–20/21 (i.e., five pairs), in *b* lines in 16/17/18 and in *a* lines in 18/19/20/21.

Internal anatomy. Septa: 7/8–13/14 thickened. Gizzard: large muscular in 5. Oesophagus: slightly dilated and vascularized in 9–15. Nephridia: vesiculate holoic, bladders elongate exiting in *c* lines; pharyngeal tufting absent. Vascularization: dorsal blood vessel single; hearts in 9,10–12 with connectives to supra-oesophageal vessel in 9–13. Spermathecae: five pairs in 5–9, elongate ovoid ampulla

on short duct with small inseminated diverticulum ectally; (Jamieson states that 7 rhs spermatheca in "Specimen 4" has several supernumerary pouches; I found this only in 6 rhs spermatheca of H, although some other rhs spermathecae had been removed and were missing from jar). Male organs: holandric, testes and funnels iridescent in 10 and 11; seminal vesicles paired, elongate and sessile on posterior septa of 9 and lobulated posteriorly in 10, and anteriorly in 12. Ovaries: as few chains of egg-strings in 13; ovisacs absent. Prostates: tubular, compact and much wound, occupying 17–19; penial setae present. Intestine: origin in 17; typhlosole absent.

Remarks. The designation of *Vesiculodrilus nivalis* is based on those specimens from Mt Kosciuszko that Jamieson (1973: 225–227, fig. 2A) described and partly figured which, despite differences from Spencer's account, he identified with *Cryptodrilus frenchi*, and one of which he used as exemplar when erecting his genus. Major differences in Jamieson's account of these Mt Kosciuszko specimens from Spencer's *Vesiculodrilus frenchi* (as augmented above) are: larger size (120–140 mm cf. 85 mm); canaliculate tanylobous prostomium (rather than epilobous); five pairs of spermathecal pores in setal *a* lines in 4/5–8/9 (erroneously stated by Jamieson, 1973: 226 to be "in 4/5–7/8") rather than just lateral of setal *a* lines; a large gizzard, rather than small or compact gizzard, in 5; and some other differences in genital markings. These gross morphological deviations from Spencer's species are confirmed by examination of those of Jamieson's specimens available for study (i.e., AM W4691–4693, Jamieson's Specimens 1–3). In view of the redescription of *V. frenchi* above, and of the differences of *Vesiculodrilus nivalis* from this, it is therefore concluded that these two species are not conspecific.

Other mainland species with five pairs of spermathecae are *Vesiculodrilus uncinatus* (Stephenson, 1933) that lacks genital markings; *V. purpureus* Jamieson, 1973 (stated to have setal ratios not differing significantly from his other Mt Kosciuszko specimens [of *V. nivalis*], although Jamieson's description of *V. purpureus* is confused: with H and P1 apparently being interchangeable with an anterior amputee specimen, now in a private collection and unavailable for study) and the closely similar *V. victoriae* (Spencer, 1892), and its varieties, all of which have median, unpaired markings; as well as *V. vallis* n.sp. that is described and differentiated below.

Etymology. The name *nivalis* (Latin) means "snowy" or "of the snow" and refers to the Snowy Mountains and Snowy River localities.

Distribution and habitat. Mt Kosciuszko, known from a single site: Alpine herbfield of *Poa caespitosa, Celmisia longifolia*, near the Snowy River at 6,200ft (1,900m). Found with earthworm species: *Graliophilus woodi* Jamieson, 1973, *Cryptodrilus fastigatus* Fletcher, 1889, *Notoscolex montiskosciuskoi* Jamieson, 1973, and *Anisochaeta celmisiae* (Jamieson, 1973). The ecology of this community is reported by Wood (1974). Specimens of three of these species have recently been identified by the current author: *Cryptodrilus fastigatus* is described below; specimens (ANIC RB.95.30.1) of *Notoscolex montiskosciuskoi* from Sawpit at the Park entrance were sent for identification by Liz Wren of National Parks and Wildlife Service (Blakemore, 1995)—these worms were being dug up and used as bait by anglers; and *Anisochaeta celmisiae* as reported by Sims & Gerard (1985: 136)—one of the species surviving introduction in the 1970's into the Highlands of Scotland in an attempt to reduce peat turf mats (see Blakemore, 1999: 184; 2000: 3).

Vesiculodrilus vallis n.sp.

Fig. 4

Material examined. HOLOTYPE: ANIC RB.97.3.5, Perisher Valley, Mt Kosciuszko, NSW, collected by Keith Vallard, "just above Perisher, in mountains". Live specimen donated by Gerard Gillespie of Queanbeyan, 5.iii.1997, (mature, complete, dissected and figured). PARATYPES: none.

External features. Body faintly canaliculate dorsally after clitellum. Length: 220 mm. Width: 15 mm. Segments: 132. Colour: (in life) dorsum dark gunmetal grey to flanks, brown from *c* to *b* lines, light brown ventrally, setal auriolae and markings pale; clitellum buff. Prostomium: closed epilobous; peristomium ventrally cleft. Clitellum: ½13–½18. Dorsal pores: minute in 3/4, open from 4/5. Setae: 8 in regular rows only in the anterior, after segment 21, *d* lines first become sinuous then other setal lines vary so that by tail all setae are very irregular but still lumbricine. Nephropores: just lateral of *c* lines in anterior from 2. Spermathecal pores: minute at anterior of segments near 4/5–8/9 in setal *a* lines. Female pores: widely paired on 14. Male pores: at centres of small mounds at interval just lateral of setal *a* lines on 18. Genital markings: on 10 and 11 large paired hollowed sucker-like discs presetal just median of *b* lines within tumid rims that extend from *a* lines to just lateral of *b* lines; in 15/16–22/23 (i.e., eight sets) paired and midventral discs median to *a-a* within slightly swollen common field.

Internal anatomy. Septa: 9/10–13/14 thickened. Gizzard: large muscular cone in 5. Oesophagus: slightly dilated and vascularized in 9–16 but not forming calciferous glands. Nephridia: vesiculate holoic, bladders elongate exiting in *c* lines; pharyngeal tufting absent. Vascularization: dorsal blood vessel single onto pharyngeal mass in 4 but forming segmentally doubled loops in segments 6 and 12 (at least); hearts in 10–12 with connectives to supra-oesophageal vessel in 7–12. Spermathecae: five pairs in 5–9, large saccular ampulla on small duct with small inseminated diverticulum ectally. Male organs: holandric, testes and funnels iridescent in mucus in 10 and 11; seminal vesicles paired racemose, elongate and sessile on posterior septum in 9, small posteriorly in 10, and small anterior rosettes in 12. Ovaries: as several egg-strings in 13; ovisacs not found. Prostates: tightly coiled tubular confined within membrane in 18; penial setae present. Intestine: origin in ½17; typhlosole absent; gut contains soil and organic matter.

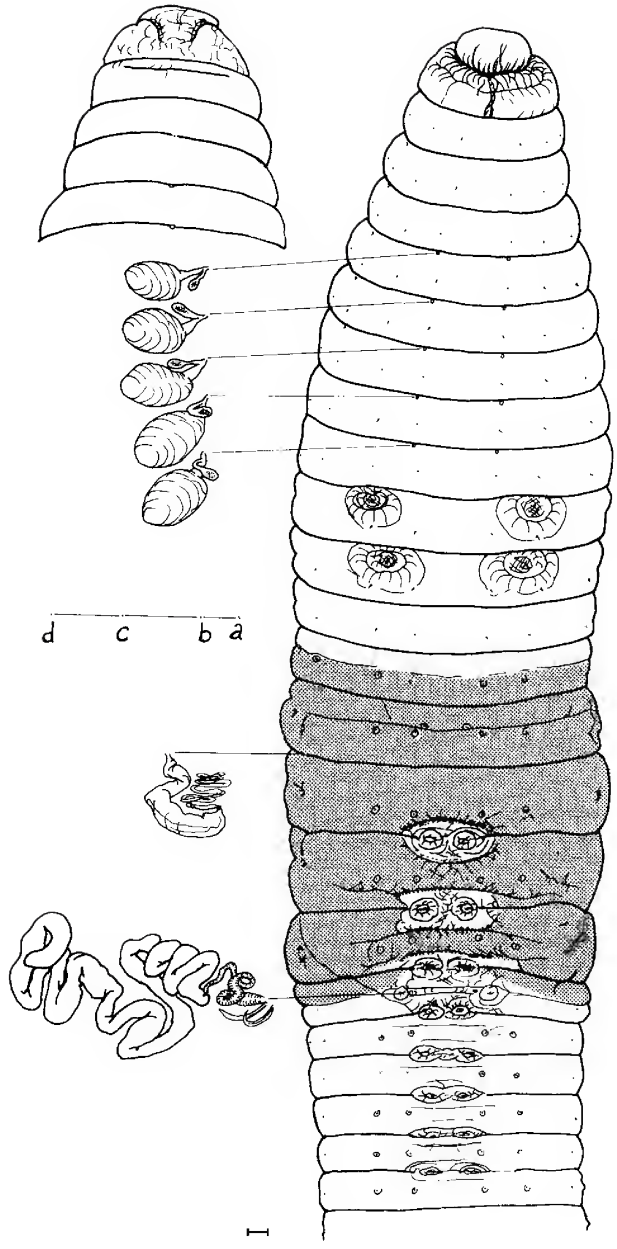

Figure 4. *Vesiculodrilus vallis* n.sp., ventral view of holotype with dorsal view of prostomium, spermathecae *in situ*; nephridial bladder in 15 lhs; and lhs prostate and penial setae in 18. Scale 1 mm.

Remarks. *Vesiculodrilus vallis* differs from the type species, *V. frenchi*, in its larger size (220 mm vs. 75–85 mm); spermathecal pores in setal *a* lines rather than just lateral of this; larger and more lateral anterior markings and narrower posterior markings (at least those in 15/16–17/18,18/19); intermittently doubled dorsal blood vessel; and by having the prostate glands coiled and confined to segment 18. Although *V. vallis* is somewhat morphologically similar to *V. nivalis* from nearby Mt Kosciuszko, it differs: in its larger size; by having epilobous, rather than tanylobous, prostomium; clitellum extending over ½13–½18, rather than 14–16; differences in the distribution of genital markings (eight posterior pairs, rather than five pairs); its doubled dorsal blood vessel; and an intestinal origin in ½17, rather than 17.

More extensive doubling of the dorsal blood vessel is described by Spencer (1892) in his Victorian species *Cryptodrilus (= Vesiculodrilus?) gippslandicus* and *Diporochaeta willsiensis*, but both of these species differ, not least, in their arrangements of genital markings. Having coiled, tubular prostates confined to segment 18 is found in *Vesiculodrilus tanjilensis* (Spencer, 1892), that also has distinctly different genital markings.

Etymology. Named after the locality (Latin, *vallis* = of the valley).

Distribution and habitat. Perisher Valley, en route to the summit of Mt Kosciuszko, has winter temperatures as low as -22°C. Because large specimens, such as *V. vallis*, often maintain deep burrows, it is possible that this species overwinters at depth. The live specimen was supplied in a container with humic sandy soil and grass in the roots of which were several tubificid microdriles (indicative of waterlogged conditions).

Genus *Megascolides* M'Coy

Megascolides M'Coy, 1878: 21; Michaelsen, 1900: 182; 1907: 160–161; Stephenson, 1930: 835; Lee, 1959: 284–285; Blakemore, 1997a: 1689–1690.
Austrohoplochaetella Jamieson, 1971: 490.
Pseudocryptodrilus Jamieson, 1972: 172.

Diagnosis. Setae 8 per segment. Clitellum typically developed over at least four segments. Male pores from tubular prostates paired on 18. An oesophageal gizzard in 5 or 6 (or 7?). Nephridia meroic, at least in the fore-body, avesiculate or vesiculate, sometimes tufted anteriorly. Spermathecae one or more pairs, each with a clavate diverticulum. Typhlosole and calciferous glands present or absent; intestinal caeca absent. Penial setae present or absent.

Type species. *Megascolides australis* M'Coy, 1878, (synonyms: *Notoscolex gippslandicus* Fletcher, 1887b; *Lumbricus australis* Vaillant, 1889) from Gippsland, Victoria. (Syntypes AM W1253–1262).

Included species

Megascolides acanthodriloides (Jamieson, 1974a) from Tasmania;
Megascolides australis M'Coy, 1878 from Victoria
Megascolides bagomaraglensis n.sp. from NSW;
Megascolides diaphanus Spencer, 1900 from Victoria;
Megascolides kendricki (Jamieson, 1971) from WA;
Megascolides maestus Blakemore, 1997a, from Tasmania;
Megascolides nokanenaensis Michaelsen, 1907 from WA;
Megascolides tenuis (Fletcher, 1889) from NSW.

Twelve additional species from Tasmania are currently in the process of formal description (Blakemore, in prep.).

Species incertae sedis

Megascolides orthostichon (Schmarda, 1861) from Mt Wellington, there is some debate as to whether this is Mt Wellington in New Zealand, or in Tasmania.

Distribution. Victoria, New South Wales, Tasmania, Western Australia, New Zealand (confined to the north of North Island). Lee (1959) describes twenty-two known *Megascolides* species fron New Zealand, but it appears that several (especially those previously attributed to the genus *Tokea*) have tubuloracemose prostates and therefore belong in *Notoscolex*. Indian species of *Megascolides* were transferred to *Scolioscolides, Barogaster* and *Travoscolides* by Gates (1940). North American species of *Megascolides* were transferred to *Driloleirus* by Fender & McKey-Fender (1990).

Remarks. The most recent discussion of this genus is found in Blakemore (1997a) where the above synonymies are discussed. A further genus, "*Dinephrus*" was proposed, but not formally described by Spencer (1900: 33) for species, like his *Megascolides diaphanus*, that have only a few nephridia per side. It is pertinent to the current study that Australian Museum specimens of *Megascolides diaphanus* Spencer, 1900 from Dimboola, Victoria (AM W1274) were unequivocally claimed by Jamieson (1972: 174) to be "type-series", indeed he designated one specimen the lectotype and others paralectotypes, whereas Jensz & Smith (1969: 99–100) list Museum of Victoria syntypes as NMV G179 and state only that Spencer's label was "Missing from the jar" (see also Remarks under *Heteroporodrilus shephardi* below).

Megascolides bagomaraglensis n.sp.

Fig. 5

Material examined. HOLOTYPE: ANIC RB.97.5.1, Maragle State Forest, NSW, Bago-Maragle, Environmentally Sustainable Management Project sample BM165, Sheet No. 8526 DGPS Long. 6030795 AMG zone 55, Lat. 617215 AMG zone 55, off Warnipers Rd., Dr P. Ryan, 10.iii.1997, (mature, dissected and figured). PARATYPES: ANIC RB.95.29.1 (P1–P3), Bago State Forest, south of Batlow, NSW (35°34'S 148°10'E), Phil Ryan, 13–17 February 1995 (three mature specimens, P1 aclitellate, dissected; P2, clitellate, dissected; P3 aclitellate, in poor condition but agreeing superficially).

External features. Body stout. Lengths (mm): 140 (H), 150 (P1, P2). Width: c. 4.5 mm. Segments: 174 (H). Colour: unpigmented in alcohol; clitellum yellow or buff. Prostomium: weakly tanylobous (H) or open epilobous (P1), faintly furrowed dorsally. Clitellum: (H, P2) 13,½13–17,½18. Dorsal pores: from 5/6. Setae: small, 8 in regular rows *c-d* widely spaced, almost equidistant with *d-d*. Nephropores: small pores sometimes seen just lateral of *b, c* and *d* lines on anterior margin of segments in anterior. Spermathecal pores: small at anterior of segments near 7/8/9 in setal *a* lines. Female pores: widely paired anteromedian to setae *a* on 14. Male pores: at centres of eye-like papillae

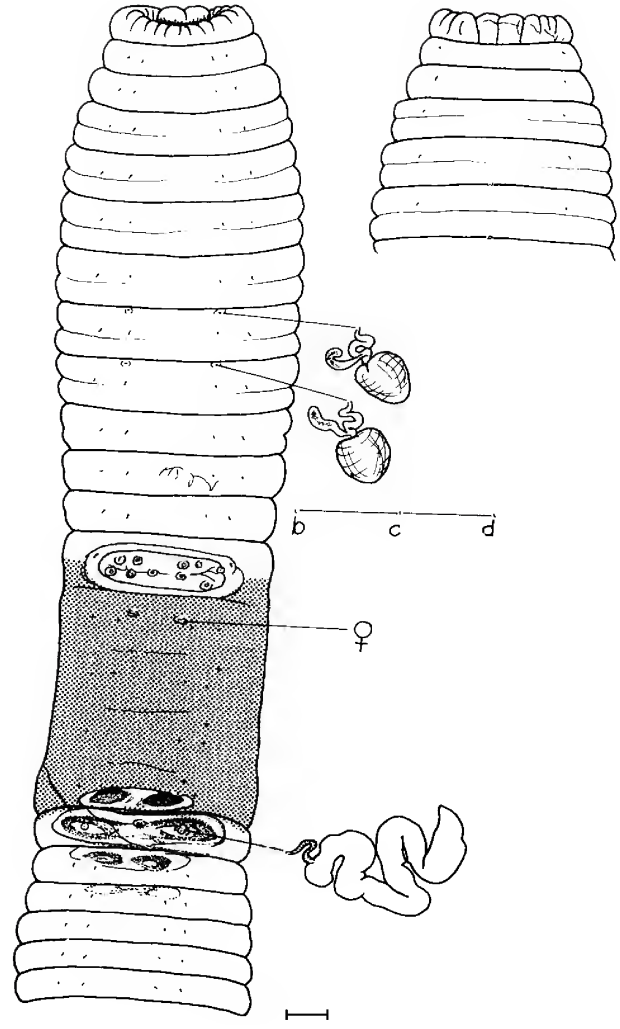

Figure 5. *Megascolides bagomaraglensis* n.sp., ventral view of holotype with dorsal view of prostomium; spermathecae; and rhs tubular prostate in 18. Scale 1 mm.

in *ab* lines within medianly conjoined elliptical darker rims on 18; small central boss often seen median to the pores. Genital markings: on 13 several small papillae laterally arranged within large sunken pad surrounded by rim that encompasses setae *b-b* and extends to 13/14 (present but less developed in P1, P2); paired dark elliptical pads postsetal in *bb* on 17; similar pads presetal on 19 and weakly repeated on 20 and (P1 only) on 21.

Internal anatomy. Septa: 5/6 thin to middle of gizzard but can be traced to base; 7/8–11/12 increasingly thickened. Gizzard: large muscular tapering cone in 5 displaced to occupy position of 6–8. Oesophagus: dilated and vascularized in 13,14–16,17 but not forming definite calciferous glands; valval in ½18. Nephridia: vesiculate meroic as lateral bands of inter-coiled tubules, two, three or more per side, ducts seen exiting in *b* and *c* lines or *c* and *d* lines, preseptal funnels not found; pharyngeal tufts in 2–3. Vascularization: dorsal blood vessel single onto pharyngeal mass in 4; hearts in 10–13 with connectives to

supra-oesophageal vessel in 8–13. Spermathecae: two pairs in 8–9, large heart-shaped ampulla on thin spiralling duct with ectally directed clavate diverticulum at junction of ampulla and duct (duct and diverticulum often enclosed in membrane). Male organs: holandric, testes and funnels iridescent in mucus in 10 and 11; seminal vesicles paired digitiform, elongate on posterior septum in 9 and anterior septum of 12. Ovaries: as several egg-strings in 13; vestigial ovisacs on anterior septum of 14. Prostates: tightly coiled thickly tubular gland on short duct (no central canal detectable in section, but branching side ducts not found either); penial setae absent. Intestine: origin in ½18; typhlosole T-shaped from 20, becoming large and c. 1 mm deep; gut contains fine soil with few grits and charcoal grains.

Remarks. Characters separating *Megascolides bagomaraglensis* from other known members of the genus, are the arrangement of genital markings (especially those in segment 13) and the distinctive shape of the spermathecae.

The prostates are construed as tubular, albeit thickly tubular with only a small central lumen, as there are no ramifying side ducts or canalicules characteristic of tubuloracemose and racemose glands. Species such as *M. bagomaraglensis*, that attain their large size by surviving for several seasons, possibly attain particularly thick glands as the columnar gland-cells regenerate from the periphery. This conclusion is extrapolated from the detailed description of tubular prostate glands by Spencer (1888: 29–30, fig. 29), Sweet (1900), and, especially, Stephenson (1930: 364–372, figs. 152–153).

In general, when regarding tubular prostates, the question to ask is whether they resemble the form of those found in the indisputably more primitive families (e.g., Acanthodrilidae), and in the primitive genera of Megascolecidae (e.g., *Pontodrilus, Plutellus, Sebastianus*). Gradations in non-tubular glands may occur: they are either obviously racemose, especially where the duct branches externally, or tubuloracemose, where internal canalicules may be found by sectioning.

Etymology. Named after the locality.

Distribution and habitat. Bago-Maragle State Forests are adjacent to and west of Kosciuszko National Park. These specimens were collected as part of a multi-disciplinary sustainability survey of forest soil ecosystems conducted by CSIRO, the Australian National University, and various state Forestry Departments. All fauna collecting was by Phil Ryan and Neil McKenzie (CSIRO Forestry, Canberra), and David Jacquier and Peter Leppert (CSIRO Land and Water). The BM165 type locality site is described as "a shallow rocky soil on metasediments in Maragle SF", the exact collection locality of the paratypes is not available, but they were obtained from "rich chocolate brown forest soil". Further site and soil survey details can be obtained from Dr Phil Ryan. *Anisochaeta rava* and *A. rubeospina* have recently been described from this locality by Blakemore (2000).

Genus *Heteroporodrilus* Jamieson

Heteroporodrilus Jamieson, 1970: 106–109; Blakemore, 1994b: 20–23.

Diagnosis. Setae lumbricine. Male pores on 18 combined with pores of racemose or tubuloracemose prostates. Gizzard well developed in 5; three to five sets of calciferous glands: paired extramural and ventrolateral, sessile or on short stalks, the last pair in 13, or (*H. bitenax*) annular in 10–13. Last hearts in 12 or 13. Nephridia vesiculate holoic; nephropores in anterior in *d, c*, or mid-*bc* lines, then, from 9 or 10 posteriorly, alternating regularly from one segment to the next in *d* and *b* lines. Spermathecae five or fewer pairs with single, or multiple diverticula.

Type species. *Cryptodrilus tryoni* Fletcher, 1890, (synonym *Woodwardiella youngi* Boardman, 1932), from Milton, Sherwood, Oxford Park, Brookfield, Toowong, all are suburbs in Brisbane; Somerset Dam, Binna Burra; Mt Glorious; Mt Mee and Nambour, all in Qld. (Type material untraceable).

Included species. Six new species are described in the current account, bringing the generic total to twenty-five species, as given in the key below. Blakemore (1994a,b) listed and described 18 known species, plus one sub-species (*Heteroporodrilus shephardi* (Spencer, 1900) *armatus* Jamieson, 1974b), and one dubious species (*Cryptodrilus fletcheri* Beddard, 1887). A subsequently described Queensland species was cursorily differentiated by Jamieson (1995: 580) thus: "*Heteroporodrilus montiserratae* is distinguished from other species of the genus in possessing four pairs of calciferous glands and three pairs of spermathecae." However, as previously shown (Blakemore, 1994a,b) this combination of characters is also found in *H. incommodus* (Jamieson & Nash, 1976) and *H. raveni* (Jamieson & Nash, 1976) as well as in *H. canaliculatus* (Fletcher, 1889), *H. mediterreus* (Fletcher, 1887b) and *H. shephardi* (Spencer, 1900). This latter species, redescribed below, was divided into sub-species by Jamieson (1974b: 87) who stated: "*H. shephardi* belongs to a group of species with four pairs of calciferous glands [and three pairs of spermathecae]".

Distribution. Widespread, especially in proximity to rivers (Fletcher, 1887b: 602). In catchments of the Murray-Darling in New South Wales through to Victoria and South Australia; Wimmera River in Victoria; Tweed River in northern NSW; and various tributaries in southeastern Queensland (Blakemore, 1994b). One species, *H. oxleyensis* (Fletcher, 1889), as redescribed by Blakemore (1994b: 29–32) from southeast Qld, has a particularly wide range having recently been found at Broulee in central coastal NSW (Blakemore, 1997b: 1838); other samples of this taxon from the Sydney region are in the Australian Museum collection (e.g., W3064, pers. obs.).

Remarks. The most recent revision is by Blakemore (1994b). Related genera are *Zacharius* Blakemore, 1997b

from northern NSW and *Woodwardiella* Stephenson, 1925 that is predominantly found in WA (although monotypic *Pseudoperichaeta* Jamieson, 1970 from Victoria is a probable junior synonym of this latter genus). These other genera lack the nephridial vesicles and calciferous glands of *Heteroporodrilus*. Furthermore, *Woodwardiella* is differentiated from *Zacharius* by having prostates that are racemose (rather than tubuloracemose), penial setae, intestine commencing from 17–19, and nephridia supposedly becoming tufted.

The above generic diagnosis is expanded slightly to permit annular calciferous glands and to note the occurrence, more commonly than previously believed, of nephropores in mid-*bc* in some anterior segments.

Key to the known species of *Heteroporodrilus*

1 Calciferous glands five pairs; spermathecae three pairs each with three diverticula (size up to 580 mm) ..... *Heteroporodrilus tryoni*

—— Calciferous glands four pairs; nephropores occasionally in 4–9 in mid-*bc* 2

—— Calciferous glands three pairs; nephropores not in mid-*bc* lines 16

2 Spermathecae three pairs 3

—— Spermathecae two pairs 11

3 Spermathecal diverticula paired 4

—— Spermathecal diverticula single (infrequently doubled) 5

4 Prostomium prolobous, dorsum canaliculate, first dorsal pore 10/11, last hearts in segment 12; small penial setae present ..... *H. canaliculatus* (Fletcher, 1889)

—— Prostomium epi-tanylobous, dorsum not canaliculate, dorsal pores from 6/7/8; last hearts in 13; penial setae absent ..... *H. kaputar* n.sp.

5 Size < 100 mm; (penial setae absent or not recorded); (Qld) ..... 6.

—— Size > 100; penial setae present; (NSW, Qld, Vic., SA) ..... 7.

6 Dorsal pores 6/7; genital markings 7–8 ..... *H. raveni*

—— Dorsal pores 5/6; genital markings 10–11 ..... *H. montiserratae*

7 Seminal vesicles in 11 & 12; few genital markings in 11–12 and 18–19; (NSW) ..... *H. mediterreus* (Fletcher, 1887b)

—— Seminal vesicles in 9 & 12; markings more numerous (Qld, NSW, Vic., SA) ..... 8.

8 Size < 135 mm; nephropores not in mid-*bc* in anterior; prostates with short ectal duct; penial setae absent; (Qld) ..... *H. incommodus* (Jamieson & Nash, 1976)

—— Size > 160 mm; nephropores intermittently in mid-*bc* in anterior; prostates with large duct to centre of (bilobed) gland; penial setae present (NSW, Vic., SA) 9

9 Size < 160 mm; prostates bilobed, duct branches externally; (Vic., SA) ..... *H. shephardi* (Spencer, 1900)

—— Size > 160 mm; prostates not so clearly divided; (NSW) 10

10 Dorsal pores from 5/6/7; spermathecal diverticula near exit of duct ..... *H. namoi* n.sp.

—— Dorsal pores from 10/11/12; spermathecal diverticula midlength on duct ..... *H. narrabri* n.sp.

11 Spermathecal diverticula single; prostates bilobed; penial setae; (Vic.) ..... *H. hirthi* n.sp.

—— Spermathecal diverticula paired; prostates not bilobed; penial setae absent; (Qld, NSW) 12

12 Spermathecal diverticula paired multiloculate 13

—— Spermathecal diverticula paired clavate 14

13 Size > 200 mm; epilobous; dorsal pores from 10/11; female pores paired; prostates racemose; (Qld) ..... *H. thompsoni* Blakemore, 1994b

—— Size < 100 mm; tanylobous; dorsal pores from 5/6; female pore single; prostates tubuloracemose; (NSW) ..... *H. editus* n.sp.

14 Size > 200 mm; epi-tanylobous; dorsal pores from 10/11; (Queensland) ..... *H. bongeen* Blakemore, 1994b

—— Size < 100 mm; tanylobous; dorsal pores from 4/5/6/7; (NSW, Queensland) 15

15 Dorsal pores from 4/5/6; spermathecae intersegmental; markings in 7 (& 10); female pores paired; prostates tubuloracemose; (NSW) ..... *H. bitenax* n.sp.

—— Dorsal pores from 6/7; spermathecae segmental; markings in 10 (or 11); female pore single; prostates racemose; (Qld) ..... *H. notatus* (Dyne, 1981)

16 Spermathecae five pairs ..... *H. jamiesoni* Blakemore, 1994b

—— Spermathecae fewer than five pairs 17

17 Spermathecae four pairs; (Qld, NSW) ..... *H. oxleyensis* (Fletcher, 1889)

—— Spermathecae fewer than four pairs 18

18 Spermathecae three pairs 19

—— Spermathecae two pairs 20

19 Spermathecal diverticula paired; (NSW) ..... *H. sloanei* (Fletcher, 1889)

—— Spermathecal diverticula single; (prostates often aborted); (Queensland) ..... *H. dioecius* (Stephenson, 1933)

20 Spermathecal diverticula paired 21

—— Spermathecal diverticula single (rarely paired) 22

21 Prostomium epilobous; markings 7–9; prostates tubuloracemose; (NSW) ..... *H. doubei* Blakemore, 1994b

—— Prostomium tanylobous; markings 10–11; prostates racemose; (Queensland) ..... *H. lamingtonensis* (Jamieson, 1970)

22 Size 400 mm; epilobous; female pores paired ..... *H. minyoni* (Dyne, 1981)

—— Size < 100 mm; tanylobous; female pore single 23

23 Prostates tubuloracemose; female pore single (NSW) ..... *H. clarkei* (Dyne, 1981)

—— Prostates racemose (bilobed); female pores paired (Qld) ..... *H. cooraniensis* (Spencer, 1900)

Heteroporodrilus bitenax n.sp.

Figs. 6, 20

Material examined. HOLOTYPE: AM W24421 (H), 6km west of Grafton, NSW, c. 29°44'S 152°52'E, Ed Easton, 18.iii.1983, "Jar 20", (mature, dissected and figured). PARATYPES: ANIC RB.98.2.12, same details as H, (P1), (aclitellate subadult, dissected); W24422, (P2), same details as H, (aclitellate subadult, inspected).

External features. Lengths, mm: 80 (H), 72 (P1), 55 (P2). Width: c. 3 mm. Segments: 180 (H), 175 (P1). Colour: unpigmented almost transparent in alcohol, clitellum cream. Prostomium: widely tanylobous. Clitellum: ½13–17. Dorsal pores: 4/5 minute, open from 5/6. Setae: 8 per segment in regular series. Nephropores: at anterior margin of segments, in *d* lines on 2–4, 5 rhs, 6 lhs, then regular alternation; in mid-*bc* lines on 5 lhs, 6 rhs, 7 lhs, 8 rhs, 9 lhs; in *b* lines on 10 rhs, 11 lhs then with regular alternation (H). Spermathecal pores: in 7/8/9 in *b* setal lines. Female pores: widely paired just anterior to setae *a* on 14. Male pores: at centres of low papillae in *b* lines on 18. Genital markings: large paired sucker-like discs occupying most of *ab* lines in 7 (H, P1, P2) and 10 (H, P2); paired postsetal discs approximately in *ab* lines in 16, 17, 19 (rhs only in P1), and 20 (H, lhs only P2); smaller secondary pair of discs median to those in 16 also present.

Internal anatomy. Septa: 5/6–9/10 increasingly thickened. Gizzard: large muscular flask-shaped in 5. Oesophagus: dilated and with deep internal lamellae in 10–13 (i.e., four sets of annular calciferous glands, in H and P1), tapering to valve in 14. Nephridia: vesiculate holoic with small sub-spherical or elongate bladders exiting at nephropores. Vascularization: dorsal blood vessel single; hearts paired in 10–12. Spermathecae: two pairs in 8 and 9, conical ampulla on narrow duct with opposed, clavate diverticula ectally. Male organs: holandric, testes and iridescent funnels in 10 and 11; seminal vesicles racemose in 9 and 12. Ovaries: palmate with several egg-strings in 13; ovisacs not found. Prostates: flattened, tubuloracemose in 18 on thin duct; penial setae absent. Intestine: origin in 15 widening in 16; typhlosole absent; gut contains coarse soil with grits and mucus.

Remarks. *Heteroporodrilus bitenax* is unique in the genus for having annular, rather than extramural, calciferous glands, requiring the inclusion of this character state in the generic diagnosis. Other distinctive characters are the two pairs of bi-diverticulate spermathecae with ingresses in *b* lines; and the arrangement of genital markings, having these anterior to the spermathecal pores is a rare occurrence in megascolecid earthworms.

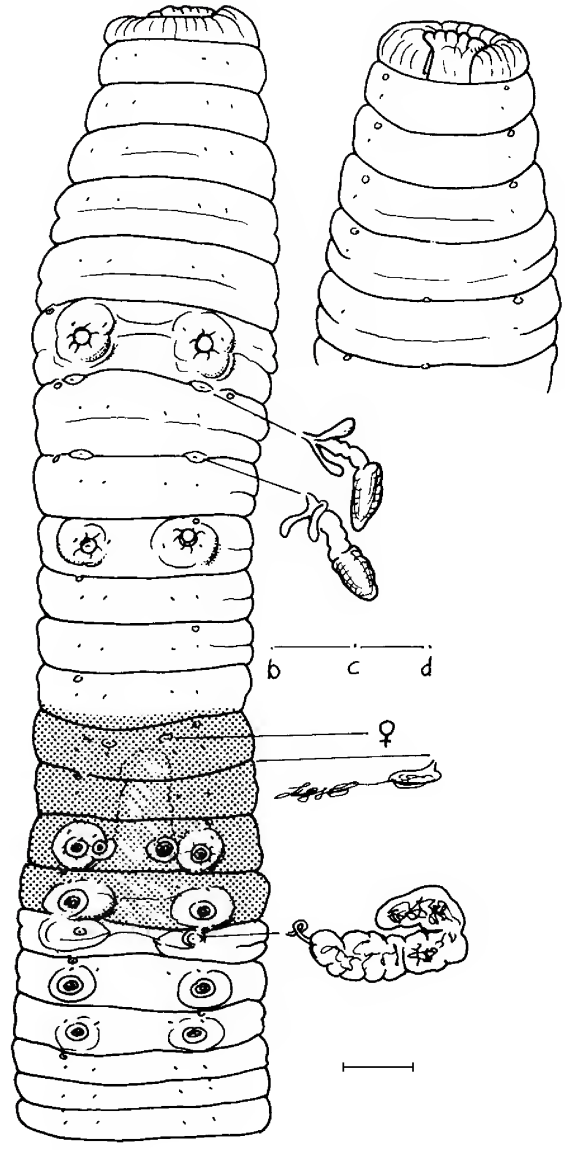

Figure 6. *Heteroporodrilus bitenax* n.sp., ventral view of holotype with dorsal view of tanylobous prostomium; spermathecae *in situ*; nephridial bladder in 15 rhs; and prostate in 18 rhs. Scale 1 mm.

Etymology. The word *bitenax* means double-gripping in Latin and refers to the sucker-like markings found on either side of the spermathecal pores.

Distribution and habitat. Grafton lies on the Clarence River in northern coastal NSW. Collection notes state from a "stand of Eucalypt".

Heteroporodrilus canaliculatus (Fletcher, 1889)

Figs. 7, 20

Cryptodrilus canaliculatus Fletcher, 1889: 1534–1536; 1890: 995–996.
Plutellus canaliculatus.–Michaelsen, 1900: 171–172.
Woodwardia canaliculatus.–Michaelsen, 1907: 162.
Heteroporodrilus canaliculatus.–Jamieson, 1970: 111–112; Blakemore, 1994b: 21–22.

Material examined. LECTOTYPE: AM W1373, two labels in jar: "*C. canaliculatus* / Forbes (H.F.) NB. Ap 24/88" [in pencil in Fletcher's hand]; "W1373 *Heteroporodrilus canaliculata* Forbes, NSW types id. E. Easton '83". (Mature specimen, amputated after segment 32, here designated the lectotype—under ICZN Article 74, as it complies with the original type description, being previously dissected and having spermathecae agreeing unequivocally with those described by Fletcher in one of his specimens). This specimen is unsuitable for external illustration due to previous dissection and handling although the spermathecae, prostates and nephridial bladders are figured herein. PARALECTOTYPES: AM W24582 (ex W1373) (14 specimens: 5 complete matures, 2 matures missing tips of tails, 1 mature posterior amputee previously dissected, 1 mature in two halves, 4 aclitellate subadults, 1 aclitellate subadult missing tail, plus two tail portions;—a complete mature, representative of the series with length 230 mm, here described and externally figured). Additional material unknown. Fletcher (1889: 1534) based his description on "twelve spirit specimens" collected by his relative Mr H.J. Fletcher (identified as "H.F." on the label), that he stated were "not well preserved and much extended". Nevertheless, most specimens remain in reasonable condition, apart from slight damage and dissection, and all agree superficially with each other and with the lectotype.

External features (compared with Fletcher's description). Body robust, marked by faint but distinct dorsal canal (indeterminate in lectotype where dissected). Lengths, mm: complete matures 210–290, subadults 130–160 (cf. 125–250 mm, Fletcher). Widths: 5–7 mm (cf. 3.5–5 mm, Fletcher). Segments: figured paralectotype 230 (cf. about 250–265, Fletcher). Colour: bleached yellow in alcohol, clitellum buff. Prostomium: prolobous in paralectotypes (peristomium "bi-annulate superiorly, not divided by the prostomium, though being ribbed all round it sometimes appears as if it were completely or half divided by the prostomium", Fletcher). Clitellum: ½13,14–17. Dorsal pores: small in 7/8, larger in 8/9 (from 8/9, Fletcher), retained on clitellum. Setae: 8 per segment in regular series. Nephropores: (in lectotype) at anterior margin of segments in *d* lines in 2, 3, 4, 7, then with regular alternation; in *c* lines in 5, 6, 8 rhs, 10, 12, 14 lhs; in mid-*bc* in 8 lhs (confirmed by internal inspection); in *b* lines in 14 rhs, 16, then regular alternation. (Paralectotypes sometimes have nephropores in mid-*bc* in several segments between 8–13). Spermathecal pores: small in 6/7/8/9 in setal *b* lines. Female pores: widely paired just anteromedian to setae *a* on 14. Male pores: paired just lateral of *b* lines on small papillae on 18. Genital markings: small indistinct paired papillae in tumid yellow pad weakly marked in 11 in middle annulus between *a-a* (seen in lectotype and paralectotype, but not described by Fletcher); broad paired papillae in *ab* in 18 on anterior and posterior annuli (latter pair absent in lectotype),

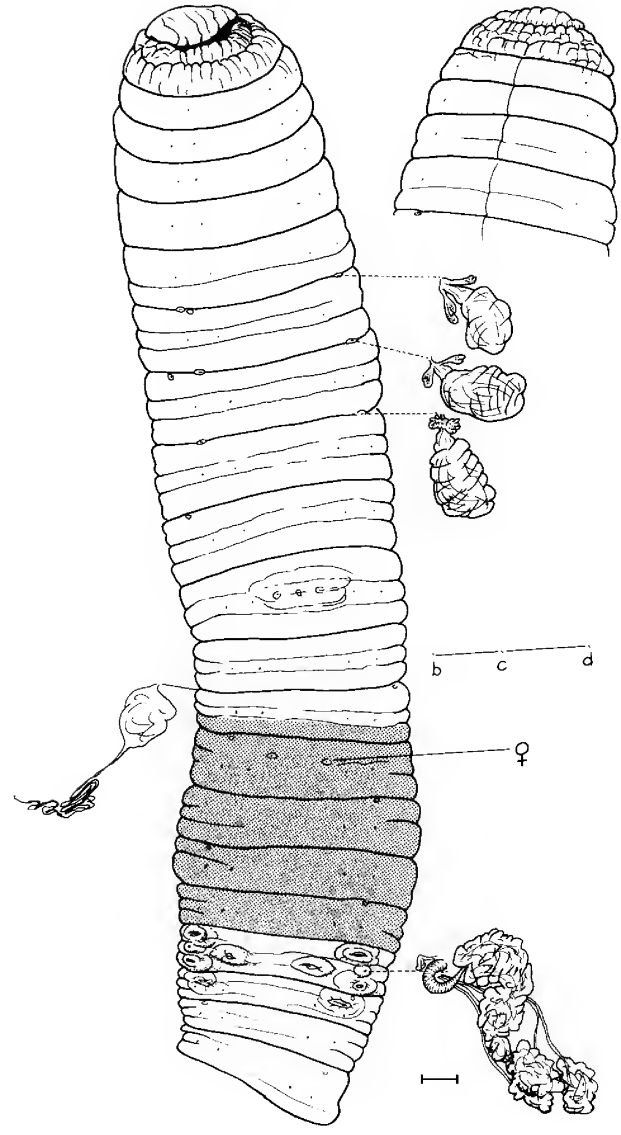

Figure 7. *Heteroporodrilus canaliculatus* (Fletcher, 1889), ventral view of a paralectotype and dorsal view of prostomium and canaliculus; nephridial bladder in 13 lhs; the spermathecae and rhs prostate with penial setae in 18 are of the lectotype. Scale 1 mm.

and on anterior annulus of 19, plus secondary pair sometimes seen median to male pores (not in lectotype).

Internal anatomy. Septa: 5/6–12/13 thickened. Gizzard: compact, muscular in 5. Oesophagus: ventrolaterally sessile calciferous glands paired in 10–13 (i.e., four pairs); narrows in 14. Nephridia: vesiculate holoic with large spherical bladders in position of nephropores. Vascularization: dorsal blood vessel single; hearts paired in 10–12. Spermathecae: three pairs in 7–9 "each with usually two short caeca [diverticula], one on each side and in front of the duct near its exit (nearer than in [*H.*] *mediterreus*), but either of these may be slightly bifid or even trifid just at the tip, or completely sub-divided into two or three, or in one case there was but a single broad flat caecum 5– or 6– lobed just

at the tip" (from Fletcher). Male organs: holandric, iridescent testes and funnels in 10 and 11 in mucus; seminal vesicles paired, racemose in 9 and 12. Ovaries: in 13; small paired ovisacs in 14. Prostates: flattened, elongate tubuloracemose in 18–19,20 on short muscular duct but with tendons from median of duct extending back to terminal lobes in 19 and 20; vasa deferentia join gland near duct; very small ensheathed penial setae seen just ventral of duct (as noted by Fletcher, 1890: 996). Intestine: origin in 15 (lectotype, cf. 16 Fletcher); typhlosole absent; gut contains remnants of brown soil.

Remarks. As these specimens correspond with Fletcher's description, despite being three more than the "twelve" specimens stated by him, there is little doubt that they are the missing type series (especially the description of the lectotype's spermathecae correspond). Slight differences from Fletcher are the weak genital markings on 11, and the intestinal origin in 15 rather than 16. Recorded for the first time are nephropores in mid-*bc* in some anterior segments, hearts in 10–12, tendons on the prostates, and lack of a typhlosole.

Fletcher distinguished *H. canaliculatus* from *H. mediterreus* as the latter species had a less robust body with fewer segments, lacked the dorsal canal, had seminal vesicles in 11 and 12 (rather than 9 and 12 as here) and because the spermathecae were noticeably different (each having only a single diverticulum). To this list may now be added last hearts in 13 (rather than 12 as here).

Distribution and habitat. Fletcher: "Forbes, NSW; from the banks of the Lachlan River". Five specimens, AM W1375 labelled, possibly in Fletcher's hand: "*Crypto canaliculatus* (?) Warren. Recd. 25/6/[18]90" are not considered conspecific as they are not canaliculate and have variations in the genital markings, amongst other differences. There is a Warren (near Dubbo) in NSW (see Other material under *H. narrabri* below).

Heteroporodrilus editus n.sp.

Figs. 8, 20

Material examined. HOLOTYPE: AM W24505 (H), Lyrebird Lookout, Mt. Warning National Park, c. 28°23'S 153°17'E, Ed Easton, 21.iii.1983, "Jar 30 Sp 4", (mature, dissected and figured). PARATYPES: none.

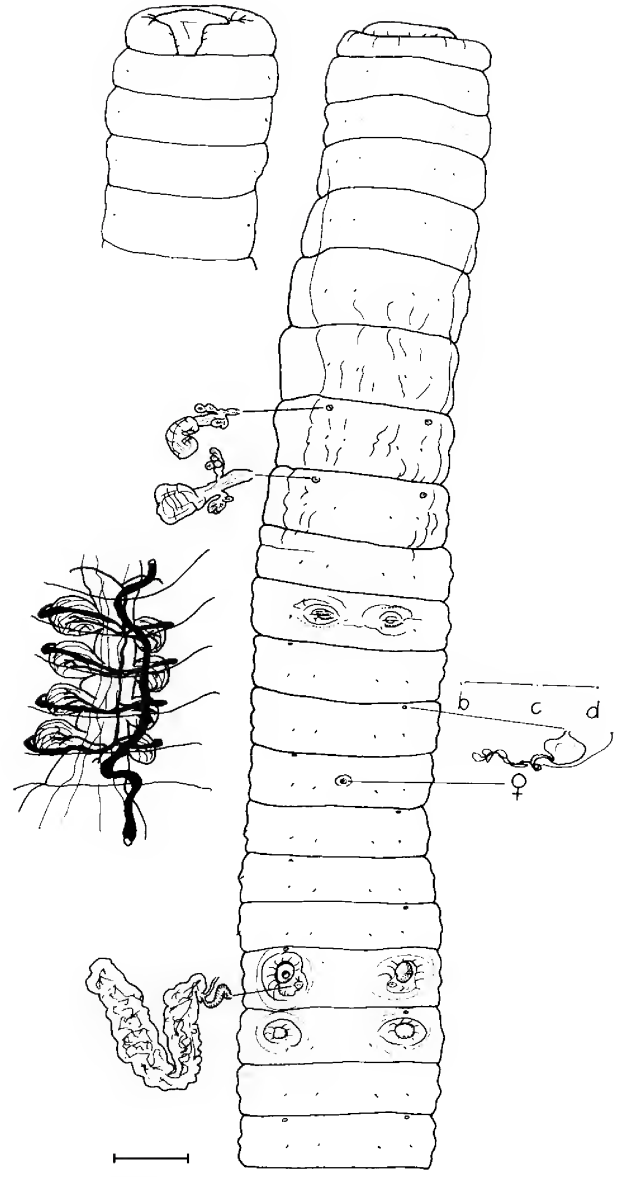

Figure 8. *Heteroporodrilus editus* n.sp., ventral view of holotype with dorsal view of prostomium; and four pairs of calciferous glands in 10–13; spermathecae *in situ*; nephridial bladder of 13 rhs; and tubuloracemose prostate in 18. Scale 1 mm.

External features. Length: 95 mm. Width: c. 2.5 mm. Segments: c. 158. Colour: unpigmented grey in alcohol, tumid ventral region of ½6–9 yellow. Prostomium: tanylobous with faint furrowing. Clitellum: not pronounced. Dorsal pores: from 5/6. Setae: 8 per segment in regular series. Nephropores: at anterior margin of segments, in *d* lines on 2–3, 4 rhs, 8 rhs, 9 lhs then regular alternation; in mid-*bc* lines on 4 lhs, 5 lhs, in *c* lines on 5 rhs, 6, 7, 9 rhs, 10 lhs; in *b* lines on 11 rhs, 12 lhs then with regular alternation; (after male pores alternations become even). Spermathecal pores: at anterior of segments 8 and 9 in setal *b* lines. Female pore: single mid-ventral just anterior to *aa* on 14. Male pores: paired on raised mounds in *ab* lines within yellow tumid areas that spread from setal *a* lines almost to *c* lines on both sides on 18. Genital markings: weakly defined paired pads in and just anterior to *ab* on 11; large sucker-like paired discs corresponding to markings around male pores centred in *b* lines presetally on 19.

Internal anatomy. Septa: 6/7–9/10 increasingly thickened. Gizzard: large muscular barrel in 5. Oesophagus: with large laterally sessile calciferous glands paired in 10–13 (i.e., four pairs). Nephridia: vesiculate holoic with small sub-spherical bladders, becoming ocarina-shaped in intestinal segments. Vascularization: dorsal blood vessel single; small hearts paired in 10–13 with connection to supra-oesophageal vessel which also projects vessels to calciferous glands. Spermathecae: two pairs in 8 and 9, saccular ampulla on

thin duct with opposed, multiloculate diverticula mid-length. Male organs: holandric, testes and iridescent funnels in 10 and 11; seminal vesicles elongate in 9 and 12. Ovaries: as numerous fine egg-strings in 13 anterior to oviducts; small ovisacs in 14. Prostates: flattened, tubuloracemose in 18–17 on short duct; penial setae absent. Intestine: origin in 15; typhlosole absent; gut contains soil with grits.

Remarks. With two pairs of bidiverticulate spermathecae, four pairs of calciferous glands, and a single female pore, *Heteroporodrilus editus* is comparable to *H. notatus*. It differs from *H. notatus* in the distribution of genital markings, lack of stalks to the calciferous glands, intestinal origin in 15 rather than 21 or 16, and prostates that are elongate rather than square.

Etymology. The word *editus* in Latin means "from on high".

Distribution and habitat. Other species found at the Mt Warning locality are listed in the account of *Digaster eastoni* below.

Heteroporodrilus hirthi n.sp.

Figs. 9, 20

Material examined. HOLOTYPE: ANIC RB.97.9.1 (H), from near Black Dog Creek on David Terrill's property near Rutherglen, Vic., c. 36°07'38"S 146°29'04"E, Jeff Hirth, 8.ix.1995, "collected from an old fence line" (mature, posterior amputee, dissected and figured). PARATYPES: MOV: F86778 (P1), same details as H, (mature, posterior amputee, dissected); ANIC RB.97.3.2 (P2), same details as H, (mature, posterior amputee, dissected).

External features. Lengths, mm: 150+ (H), 130+ (P1), 80++ (P2). Width: c. 6 mm. Segments: 100+ (H). Colour: unpigmented light grey in alcohol. Prostomium: epitanylobous with faint furrowing. Clitellum: 14–½17. Dorsal pores: minute from 8/9 (H) or from 7/8 (P1, P2). Setae: 8 per segment in regular series. Nephropores: at anterior margin of segments (H) in *d* lines on 2–4, 6 rhs, 7, 9 then regular alternation; in mid-*bc* lines on 5, 6 lhs, and 8; in *b* lines on 10, 12, then with regular alternation; (P1 and P2 basically agree except the pores are asymmetrical in P1). Spermathecal pores: 7/8/9 in setal *b* lines. Female pores: paired just anteromedian to setae *a* on 14. Male pores: paired just lateral of *b* lines on prominent papillae on 18. Genital markings: large but flat paired pads in *ab* presetally in 11 and 12 (all specimens, except on rhs only on 11 in P2); small paired discs postsetal in *aa* on 17 near 17/18 (H) or with two pairs of discs posteromedian to setae *a* and setae *b* on 17 (P1) or absent from 17 (P2); larger sucker-like pads near intersegmental furrow median of *ab* anteriorly in 18 and 19 each with smaller pair of discs posteriorly and also posterolaterally, the latter pair just anterior to male pores on 18 (H) and with additional pair posterior to the male pores (P1).

Internal anatomy. Septa: 6/7–12/13 increasingly thickened. Gizzard: in 5 muscular barrel, occupying 7–8. Oesophagus: small ventrolaterally sessile calciferous glands paired in 10–13 (i.e., four pairs); valval in 14. Nephridia:

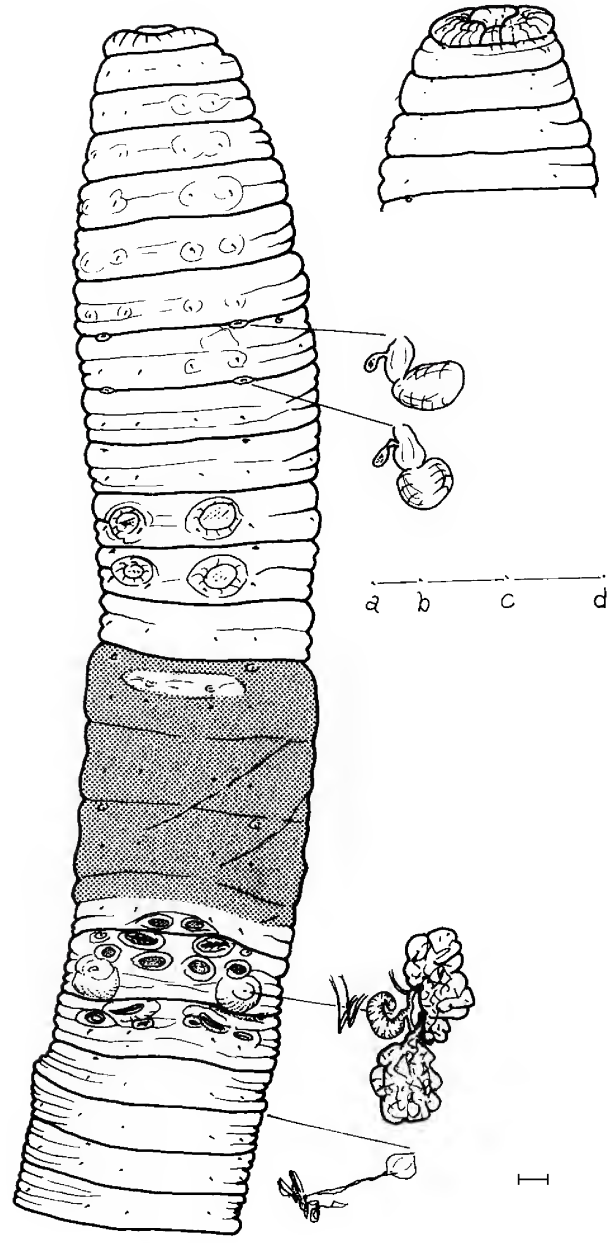

Figure 9. *Heteroporodrilus hirthi* n.sp., ventral view of holotype with dorsal view of prostomium; spermathecae *in situ*; bilobed racemose prostates in 17–19 with penial setae; and nephridial bladder in 21 rhs. Scale 1 mm.

vesiculate holoic with small spherical bladders (not found in clitellar region). Vascularization: single dorsal blood vessel onto pharyngeal mass; large hearts paired in 10–13 with connection to supra-oesophageal vessel that itself connects with calciferous glands on each side. Spermathecae: two pairs in 8 and 9, as flattened heart-shaped ampulla on muscular duct with rudimentary club-shaped diverticulum approximately mid-length. Male organs: holandric, testes and iridescent funnels in 10 and 11 (obscured by mucus); paired seminal vesicles small racemose (H) or vestigial in 9 (P1 and P2), absent from 11,

and larger in 12 (all specimens). Ovaries: as long egg-strings in 13 anterior to oviducts; ovisacs absent from 14. Prostates: flattened, racemose in 17–19; large duct to middle of gland bifurcates to incompletely separated anterior and posterior lobes, the anterior fork joined by vas deferens close to junction with gland; penial setae present. Intestine: origin in 15; typhlosole absent; gut contains fine textured loamy soil with fibrous root fragments and seed cases plus a few red quartz grits and occasional large pebbles (one 3 mm diameter in H).

Remarks. *Heteroporodrilus hirthi* is morphologically close to *H. shephardi*, as redescribed herein, especially with regard to the genital markings and shape of the prostates and spermathecae. What distinguishes *H. hirthi* are two, rather than three, pairs of spermathecae; the delayed onset of dorsal pores; and the apparently reduced seminal vesicles in 9. Having two pairs of spermathecae and four pairs of calciferous glands are features shared with several other species that are differentiated in the key above.

Etymology. Named after the collector, Dr Jeff Hirth.

Distribution and habitat. Rutherglen, Vic. is near the Murray River.

Heteroporodrilus kaputar n.sp.

Figs. 10, 20

Material examined. HOLOTYPE: AM W24403 (H), Mt Kaputar National Park, NSW, c. 30°10'S 150°10'E, Ed Easton, 29–30.iii.1983; four labels in jar: "Mt Kaputar N. Pk, 30 March, 1983", "Mt Kaputer [sic] NP—Junction of Mt K + Dawson's Spring Rd 29/3/83", "*Diporochaeta* sp. nov.?", "Jar 39 Sp 6 Mt Kaputer [sic]", (mature, posterior amputee, dissected and figured). PARATYPES: ANIC RB.98.2.1, (P1), same details as H, (mature, complete but with slight anterior damage, dissected); W24405, (P2), same details as H, (aclitellate mature posterior amputee, dissected); ANIC RB.98.2.2, (P3), same details as H, (aclitellate mature); W24406, (P4), same details as H, (subadult or juvenile); ANIC RB.98.2.3, (P5), same details as H, (juvenile); W24407, (P6–P9), (in original jar with labels), same details as H, (four immature specimens that agree superficially plus four tail fragments); AM W24408, (P10–P12), same location as H, labelled "Dawson's Spring Mt Kaputar N.Pk. 30 March, 1983", "Ed Easton Collection", "AM 40 *Diporochaeta* sp2 nov. (see 39) dark brown/purple dorsally alt nephs", "Jar 40 Sp 6 Mt Kaputer [sic]", (three aclitellate mature specimens, one dissected here).

External features. Body stout, not dorsally canaliculate, tail sometimes square in section. Lengths, mm: range of matures 150–270; 140+ (H), 270 (P1), 180 (P3), 175 (P4), 125 (P5), 90–130 (P6–P9), c. 150 (P10–P12). Width: c. 10 mm. Segments: 190 (P1), 169 (P3). Colour: dark dorsally in life (see W24408 label), uniform brown or golden in alcohol, clitellum russet. Prostomium: epi-tanylobous (i.e., can appear closed epilobous but often has furrows extending to intersegment). Clitellum: 14–17. Dorsal pores: open from 7/8. Setae: 8 per segment in regular series. Nephropores: at anterior margin of segments, in *d* lines on 2–4, 8, 10 then regular alternation; in *c* lines on 5, 6; in mid-*bc* lines on 7, 9; in *b* lines on 11, 13 then with regular alternation (in H).

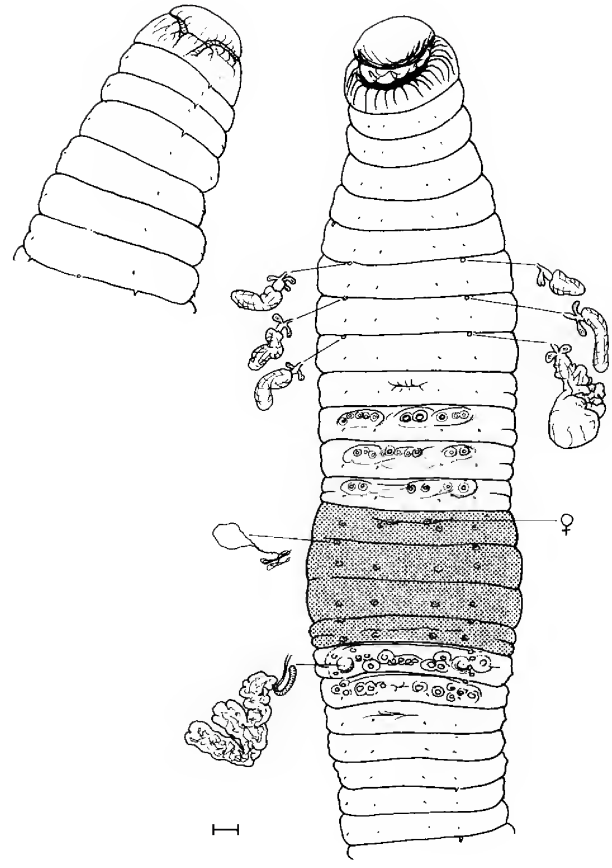

Figure 10. *Heteroporodrilus kaputar* n.sp., ventral view of holotype with dorsal view of prostomium; spermathecae showing pseudovesicle attached to 9 rhs ampulla; nephridial bladder in 15 lhs; and prostate with vasa deferentia in 18–20. Scale 1 mm.

Spermathecal pores: at anterior margin near 6/7/8/9 in setal *b* lines. Female pores: widely paired anteromedian to *a* setae on 14. Male pores: at centres of small papillae in *b* lines on 18. Genital markings: on 11 (not P1, P4, P5, P10), and/or on 12 and 13 (all matures and juveniles), presetal battery of irregularly numerous small discs between *b-b*; on 18 and 19 (all matures and juveniles) whole ventral aspect to just lateral of *b* with several irregularly arrayed small discs (sometimes reduced in number on 19).

Internal anatomy. Septa: 7/8/9–12/13/14 only slightly thickened; attached to the anterior base of septum 8/9 are large paired glands or pseudovesicles of unknown function as no connection found to oesophagus nor to male organs. Gizzard: compact muscular in 5. Oesophagus: with ventrolaterally sessile extramural calciferous glands in 10–13 (i.e., four pairs); valval in 14–½15. Nephridia: vesiculate holoic with large spherical bladders exiting at nephropores; not tufted in anterior. Vascularization: dorsal blood vessel single onto pharyngeal mass in 4; hearts paired in 10–13 from supra-oesophageal vessel in 10–13 that also supplies calciferous glands. Spermathecae: three pairs in 7–9 (in H the 9 rhs spermathecae is displaced anteriorly into segment 8 although it still exits in 8/9 and is intimately implicated with 8 rhs pseudovesicle—see Fig. 10), elongate ampullae

on short ducts with small opposed or single diverticula mid-length (i.e., diverticula paired except in H 7 lhs has small supernumerary diverticulum; in H 7 rhs has single but slightly bifid diverticulum on spermatheca, single diverticula also in P1 in 7 and 9, P2 in 7, and P10 in 7 and 9). Male organs: holandric, testes and iridescent funnels in mucus in 10 and 11; small seminal vesicles saccular in 9 and 12. Ovaries: palmate with fine egg-strings in 13; small ovisacs in 14. Prostates: flattened, tubuloracemose in 18–20 on thin duct; penial setae absent. Intestine: origin in ½15 (H, P2, P10) or 16 (P1); typhlosole absent; spiralling gut contains grey soil with few grits and charcoal, and some fibrous material.

Remarks. *Heteroporodrilus kaputar* has four pairs of calciferous glands and three pairs of spermathecae that often have paired diverticula (sometimes single or triple). It therefore resembles the similarly large *H. canaliculatus*, but it differs notably in the arrangement of small disc-like markings in (11), 12, 13, 18 and 19. Another distinctive feature is the large pair of pseudovesicles (of unknown function) in segment 8, that are larger than the seminal vesicles in 9 and 12. The intestinal origin appears to vary between ½15 and 16.

Etymology. Named after the type locality.

Distribution and habitat. Mt Kaputar National Park is just east of Narrabri en route to Warialda, NSW; it is in the catchments of the Namoi and Gwydir Rivers, tributaries of the Murray-Darling.

Heteroporodrilus mediterreus (Fletcher, 1887b)

Figs. 11, 20

Cryptodrilus mediterreus Fletcher, 1887b: 602, 614–616.
Cryptodrilus mediterreus.–Fletcher, 1889: 1535–1538; 1890: 995–996.
Woodwardia mediterreus.–Michaelsen, 1907: 162.
Heteroporodrilus mediterreus.–Jamieson, 1970: 117–120, figs. 4a,b,e–g,9d,10e; Blakemore, 1994b: 21–23.

Material examined. LECTOTYPE: AM W1338, part of Fletcher Collection donated to Australian Museum; sample contains two labels: "*Crypto mediterreus* H.F. R. Darling / Big specimen—Gragin T.G.S." [in Fletcher's hand]; "W.1338 *Heteroporodrilus mediterreus* Gragin & Warialda Pres. J.J. Fletcher". Fletcher (1887b: 616) gives locality as "The banks of the Darling River between Bourke and Brewarrina, NSW", the latter c. 29°30'S 140°30'E, collected by Mr H.J. Fletcher (identified as H.F. on label). The original sample contains 17 specimens that were shrivelled and in less than ideal condition: 6 clitellate matures (3 previously dissected); 6 aclitellate matures (one dissected, one damaged); 3 anterior portions; an immature that measures 38 mm × 2.5 mm and has 134 segments; a large clitellate mature that is darker and more square and is undissected but broken into about four pieces that combined measure about 80 mm long × 10 mm wide; plus 3 tail portions. Most of these specimens are syntypes, one of the matures that was previously dissected is redescribed, figured, and is here designated the lectotype. The remaining specimens from AM W1338 are now PARALECTOTYPES: AM W24579, (ex W1338), (14 specimens and 3 tail portions) and W24580 (the immature specimen). (The larger specimen, W24581, from Gragin according to the label, is not a syntype as it did not form part of the original description and the label indicates it was from a different locality). Arguments for these decisions are presented in Remarks below. Jamieson (1970: 119) inspected W1338, but recorded only six specimens, did not appreciate its significance as the type series, and misinterpreted both the type localities and the original label: erroneously stating they were all from "Gragin and Warialda, Victoria". Additional material unknown.

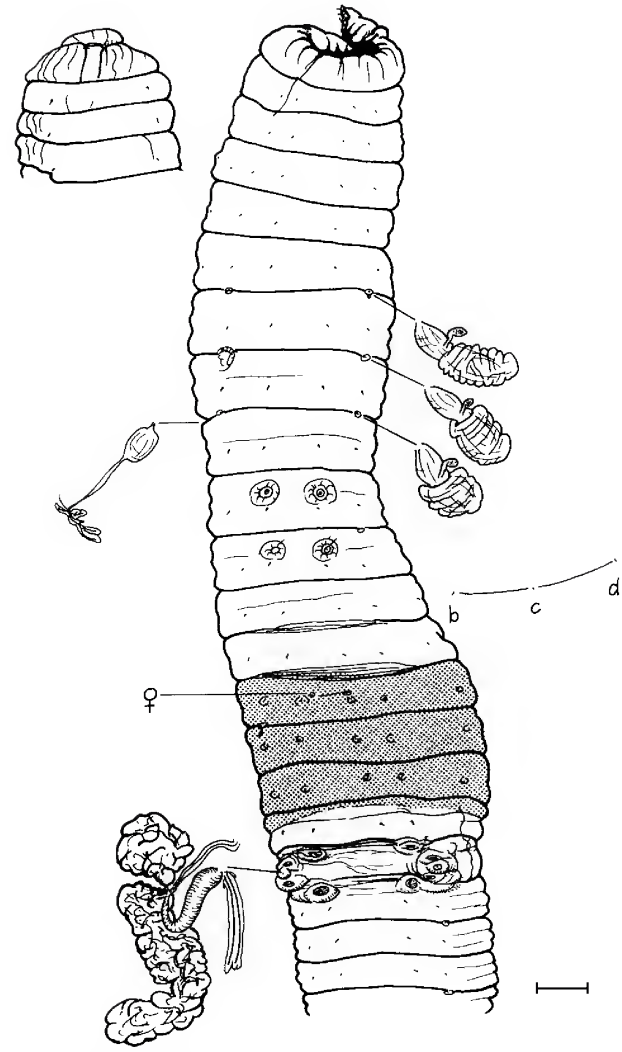

Figure 11. *Heteroporodrilus mediterreus* (Fletcher, 1887), ventral view of dissected lectotype; spermathecae *in situ*; nephridial bladder in 9 lhs; and lhs bilobed prostate with vasa deferentia and long penial setae in 17–20, 21; the dorsal view of prostomium is of a paralectotype. Scale 1 mm.

External features (compared to Fletcher's description). Body fairly stout, not dorsally canaliculate. Lengths, mm: 105 (lectotype); other clitellates 80–100; aclitellates 65–100 (cf. 73–110 mm, Fletcher). Width: 4–5 mm (ditto Fletcher). Segments: 144 (lectotype), (cf. 130–150, Fletcher). Colour: yellow-brown in alcohol; clitellum buff (cf. "above sooty-brown, darkest in the anterior portion of

the body, especially in front of the clitellum, lighter below, the clitellum with a tinge of red or purplish", Fletcher). Prostomium: (in paralectotypes, lectotype damaged) epitanylobous, i.e., looks tanylobous but peristomium is also deeply furrowed transversely (Fletcher concluded that the longitudinal groovings were not part of the prostomium). Clitellum: weak ½13,14–16,½17. Dorsal pores: from 5/6 or 6/7 (ditto Fletcher). Setae: 8 per segment in regular series. Nephropores: (difficult to discern) at anterior margin of segments, in *d* lines in 2–4, 6 lhs?, 7 rhs, 8 lhs, 9 rhs, then alternating; in *c* lines in 5, 6 rhs?, 8 rhs?, 9 lhs; in *b* lines in 10 rhs, ll lhs, then alternating. Spermathecal pores: 6/7/8/9 in *b* setal lines. Female pores: widely paired just anteromedian to setae *a* on 14. Male pores: paired just lateral of setal *b* lines on conspicuous papillae on 18. Genital markings: (lectotype) two pairs of papillae just anterior to setae *a* in 10 and 11; two pairs of papillae in *ab* lines at anterior margins of 18 and 19; two pairs of small papillae are on porophores just median and adjacent to male pores on 18; (mature paralectotypes agree with the lectotype, some have slight tumidity around the spermathecal pores in 6–9, as described by Fletcher, although the lectotype does not).

Internal anatomy. Septa: 5/6 to base of gizzard, 6/7–13/14 some thickening. Gizzard: muscular barrel with anterior crop in 5. Oesophagus: small ventrolaterally sessile calciferous glands paired in 10–13 (i.e., four pairs, slightly damaged in lectotype). Nephridia: vesiculate holoic with small spherical bladders in position of nephropores. Vascularization: dorsal blood vessel single; hearts paired in 10–13. Spermathecae: three pairs in 7–9, pouch-like ampulla on thick duct with rudimentary club-shaped diverticulum attaching at some distance from the exit (lectotype 8 lhs removed and missing from jar). Male organs: holandric, iridescent testes and funnels in 10 and 11 in mucus; seminal vesicles very small paired, racemose anteriorly in 11 and 12 (i.e., none recorded in 9). Ovaries: in 13 as usual; ovisacs not found. Prostates: flattened, racemose in 17–20,21; with smaller anterior and larger posterior lobes, ductules from each combine and joined with vasa deferentia at muscular duct; large paired sacs each containing delicate, curved penial setae about 2.4 mm long and minutely spinose towards tips (in lectotype, rhs prostate and setae removed and missing from jar). Intestine: origin in 15 (in paralectotype that agrees externally with lectotype, gut removed from lectotype after 14), (cf. in 18, Fletcher); typhlosole absent (lectotype and paralectotype); gut contains fine light grey soil, some sand grains and much fibrous material (root hairs?).

Remarks. Fletcher (1887b: 614–616) based his description on "Ten (spirit) specimens" and "A young specimen 4.2 cm long, and 2½ mm. wide [that] comprises 132 segments" that were "sent to me by my relative Mr H.J. Fletcher, who found one by accident, and obtained the others by digging for them." The label accompanying AM W1338 shows them to be from the Darling River locality with the named collector ("H.F."). The above specimens, although numbering a few more, agree with each other and concur with Fletcher's description on most points, except that the intestine commences in 15 rather than 18. Moreover, the dimensions of the immature specimen (W24580) are especially close, reinforcing the syntype status.

The anomalous larger specimen (W24581) is a damaged mature that has genital markings in 10 and 11 but is otherwise in too poor condition to identify with certainty. It is identified with a different locality (Gragin is near Warialda, NSW, about 350 km east of Brewarrina), and a different collector ("T.G.S." is probably Mr T.G. Sloane who Fletcher [1889: 1523, 1537, 1541] states also collected samples of earthworms from Coonabarabran and Narrabri, central NSW, both localities en route to Gragin). It is therefore not considered a syntype and may well be a different species although it is now too damaged to decide.

H. mediterreus has many characters in common with *H. shephardi* (Spencer, 1900), not least: four pairs of calciferous glands, three pairs of spermathecae each with a single, small diverticulum, and similar distributions of genital markings. What distinguishes *H. mediterreus* are the seminal vesicles in 11 and 12, rather than the more usual 9 and 12. (Other differences from *H. shephardi* and from *H. canaliculatus* are made under these species' descriptions).

Distribution and habitat. Fletcher: "The banks of the Darling River between Bourke and Brewarrina, NSW". For reasons given in Remarks above, Gragin and Warialda are no longer considered type-localities.

Dyne (1984: 266) believed that a specimen (NMV G70) listed under *Cryptodrilus queenslandicus* in Jensz & Smith (1969: 90) was referable to *H. mediterreus*. If confirmed, this specimen collected from Gayndah, Qld would greatly extend the distribution of this species although it is probable, in view of the subsequent generic changes and number of new taxa now added, that this specimen is not conspecific.

Heteroporodrilus namoi n.sp.

Figs. 12, 20

Material examined. HOLOTYPE: ANIC GD.95.114.1 (H), Walgett, NSW, c. 30°10'S 148°0'7E, collector Tom McCredie, November, 1991, "MYALL", (the original plastic container in which the specimens were provided, had to be cut open to remove them during curatorial processing by the author in 1995, they had not previously been inspected), (complete mature, dissected and figured). PARATYPE: ANIC GD.95.114.2 (P), same details as H, (mature, dissected). Specimens: ANIC RB.97.5.2 (S1–S4), Walgett, NSW, collector Y. Chan of NSW Dept. Agriculture, October, 1994 (four slightly macerated specimens, complete matures but clitella not developed, one dissected).

External features. Body ventrally tumid 4–30, deeply serrated ventrally in 5–12; not canaliculate dorsally (H and P). Lengths, mm: 280 (H), 270 (P), c. 300 (S1–S4). Width: 6–8 mm. Segments: 194 (H), 150 (P and S1). Colour: bleached straw in alcohol. Prostomium: weakly tanylobous with faint dorsal furrow (difficult to determine as remainder of peristomium also faintly furrowed). Clitellum: ½13,14–½17. Dorsal pores: small in 5/6, larger from 6/7 (H, P and S1–4). Setae: 8 per segment in regular series. Nephropores: (in H) at anterior margin of segments in *d* lines on 2–4, 6, 8, 10, then regular alternation but skips in mid-body; in mid-*bc* (or just ventral of *c* lines?) on 5, 7, 9 rhs; in *b* lines on 9 lhs, 11, 13, then

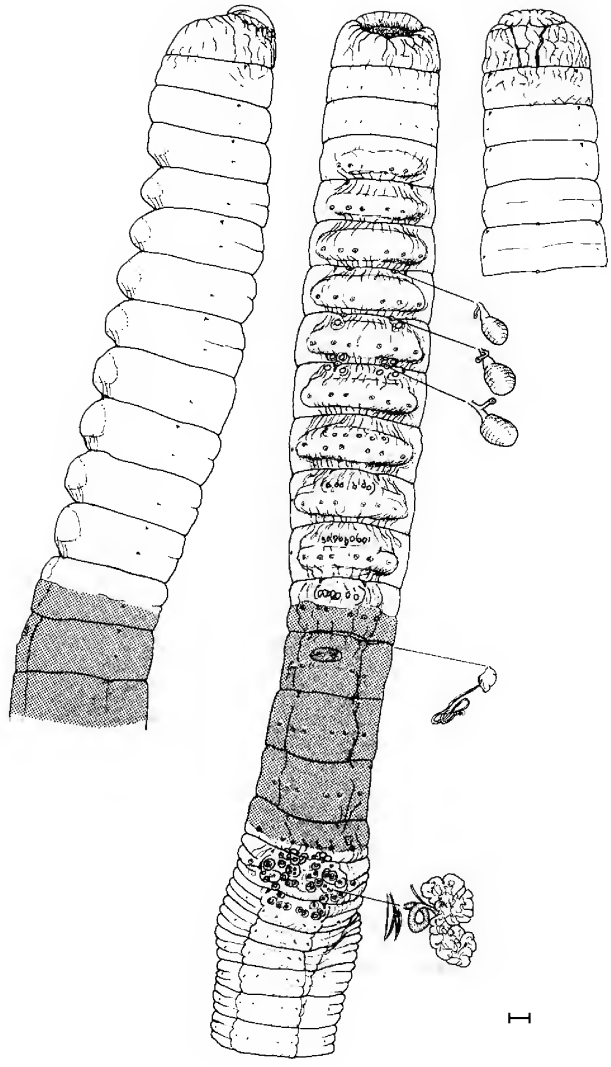

Figure 12. *Heteroporodrilus namoi* n.sp., lateral and ventral view of holotype with dorsal view of tanylobous prostomium; spermathecae *in situ*; nephridial bladder in 14 rhs; and racemose prostate with vasa deferentia and long penial setae in 18–19. Scale 1 mm.

with regular alternation but skips in mid-body; (in P) in *d* lines on 2–4, 6, 8, then regular alternation; in mid-*bc* (or *c*?) lines on 5, 7, 9; in *b* lines on 11, (13?), 15, then with regular alternation; (S1–4) have the typical arrangement of *d* lines in 2–4, then with regular alternation from 7; in *c* lines in 5,6, and 8; and in *b* lines alternately from 10. Spermathecal pores: 6/7/8/9 in setal *b* lines. Female pores: paired just anteromedian to setae *a* on 14. Male pores: superficial, paired just lateral of *b* lines on 18; tips of penial setae protrude. Genital markings: (H and P) tumid mid-ventrally between *cc* on 4–13 with presetal row of papillae in *bb* lines in 10–13; small papillae near spermathecal pores in 8 and 9 (H) or in 6–9 (P); (in H and P) postsetal on 17 and 18, rows of small papillae in *b-b* lines; the whole of 18 with complex arrangement of numerous small papillae; on 19 presetal row of papillae in *b-b*. (Markings not obvious in S1–4 although possibly some tumidity ventrally in 6–12 and in 17–19).

Internal anatomy. Septa: 5/6–13/14 increasingly thick, then thin. Gizzard: in 5 muscular onion-shaped. Oesophagus: small ventrolaterally sessile calciferous glands paired in 10–13 (i.e., four pairs); valval in 14. Nephridia: vesiculate holoic; spherical bladders in position of external nephropores, after clitellum dorsal bladders have lobe on both sides of septum. Vascularization: dorsal blood vessel single; hearts paired in 10–13 with connection to supra-oesophageal vessel in 12–13. Spermathecae: three pairs in 7–9, pouch-like ampulla on tapering duct with rudimentary club-shaped diverticulum from exit of duct, not extending as far as ampulla. Male organs: holandric, iridescent testes and funnels in 10 and 11 in mucus; seminal vesicles racemose (either irregular in outline or saccular) in 9 and elongate in 12. Ovaries: small palmate with numerous egg-strings in 13; small paired ovisacs in 14 (seen in H). Prostates: flattened, racemose in 18–19 but not divided into separate lobes; duct to middle of gland with vasa deferentia joining junction with gland; curving penial setae present. Intestine: origin ½15, but difficult to determine as intestinal wall same thickness in posterior of 15 and in 16, while notable expansion occurs only in 16; typhlosole absent; gut contains soil with some organic matter and grits.

Remarks. *Heteroporodrilus namoi*, with four pairs of calciferous glands and three pairs of spermathecae, is similar to several other species in the genus (differentiated in the key above). While superficially resembling *H. mediterreus* or *H. canaliculatus*, it differs thus: from *H. mediterreus* by having seminal vesicles in 9 and 12 (rather than 11 and 12), the spermathecal diverticula are near the exit of the duct (rather than nearer the junction with the ampulla) and the prostates are not bilobed nor as extensive; from *H. canaliculatus* it differs by having spermathecal diverticula that are single rather than paired or multiple.

The arrangement of genital markings in *H. namoi* resemble those of both *H. mediterreus* and *H. shephardi*. However, they are more extensive than the "swollen ventral portion" in 6–9 described for *H. mediterreus* and not paired or single in 7–12 as in *H. shephardi*, but are smaller and much more numerous, both in the anterior and around the male field, than in either species. All three species have a tendency towards prostates that are divided into two lobes with duct near the mid-point.

Etymology. After locality—the Namoi River.

Distribution and habitat. Walgett in northern central NSW is approximately midway between Bourke and Narrabri (the known ranges of *H. mediterreus* and of *H. narrabri*, respectively) it stands at the confluence of the Namoi River and the Barwon River that flow into the Murray-Darling River system. Tom McCredie (per. comm., 9.x.1998) found the specimens on the soil surface after heavy rain in "Myall" (*Acacia snowdenii*) wattle scrub. A recent study by Friend & Chan (1995) considered the ecology of this worm under cultivated soils in the Walgett area.

Heteroporodrilus narrabri n.sp.

Figs. 13, 20

Material examined. HOLOTYPE: ANIC RB.97.3.1 (H), Narrabri, NSW, under irrigated cotton that was unsprayed for 3 years, Australian Cotton Research Institute ("ACRI, B16"), January, 1996 (mature, dissected and figured). PARATYPE: ANIC RB.97.3.2 (P), same details as H, (mature, dissected). Specimens: ANIC RB.98.12.1, (S1, S2), two mature specimens (180–190 mm) from Trangie, NSW collected by Dr Yin Chan, 10.vi.1998—both agree superficially, and one dissected agreed internally except that seminal vesicles were found in 12 only. Specimens AM W1375 from Warren (near Dubbo), NSW noted under *H. canaliculatus* above also agree externally and may be conspecific with *H. narrabri* although confirmation of this requires further work.

External features. Lengths, mm: 330 (H), 265 (P), 190 (S1). Width: 6–8 mm. Segments: 200 (H). Colour: with faint grey tinge in alcohol. Prostomium: narrowly tanylobous. Clitellum: 14–½17. Dorsal pores: from 10/11 rudimentary, open from 11/12 (H, P, S). Setae: 8 per segment in regular series, small in posterior. Nephropores: at anterior margin of segments, (H) in *d* lines on 2–4, 7, 9 then regular alternation but doubles up on 21 rhs; in *c* lines on 5 lhs; in mid-*bc* lines on 5 rhs, 6, 8, 10 rhs; just lateral of *b* lines on 10 lhs, 11, then with regular alternation but doubles up on 21 lhs; (P) in *d* lines on 2–4, 6, 8, then regular alternation; in mid-*bc* lines on 7, 9; just lateral of *b* lines on 11, then with regular alternation; (in S1 in mid-*bc* in 5, 7 and 9). Spermathecal pores: 6/7/8/9 in *b* setal lines. Female pores: paired just anteromedian to setae *a* on 14. Male pores: paired just lateral of *b* lines on small papillae on 18. Genital markings: mid-ventral, presetal rows of papillae in *aa* on 9,10–13 thus: (H) two papillae on 12 otherwise c. six papillae on 9–13; (P) three papillae on 10, five on 11, none on 12, eight on 13; (H and P) postsetal on 17 and 18 two pairs of papillae in approximate line with *a* and *b* setae; presetal on 18 and 19 pair of small sucker-like pads in *ab* lines each with median disc; on 18 above and between male pores, several small papillae.

Internal anatomy. Septa: 6/7–13/14 with some thickening. Gizzard: in 5 muscular barrel, preceded by crop in 4. Oesophagus: small ventrolaterally sessile calciferous glands paired in 10–13 (i.e., four pairs); valval in 14. Nephridia: vesiculate holoic with small spherical bladders in anterior, bladders not found in clitellar region; in posterior bladders bilobed either side of septum when in *d* lines and spherical when in *b* lines. Vascularization: dorsal blood vessel single; hearts paired in 10–13 with connection to supra-oesophageal vessel which also connects with calciferous glands. Spermathecae: three pairs in 7–9, as pouch-like ampulla on duct with rudimentary club-shaped diverticulum mid-length. Male organs: holandric, iridescent testes and funnels in 10 and 11 in mucus; seminal vesicles small paired, racemose in 9 and larger in 12. Ovaries: small palmate with numerous oocytes in 13; small pair of ovisacs in 14. Prostates: flattened, racemose in 18–19 (H) or 17–20 (P); duct to middle of gland with vasa deferentia joining duct near junction with gland; penial setae present. Intestine: origin in 15 (H) or ½15 (P); typhlosole absent; gut contains fine (clay?) soil.

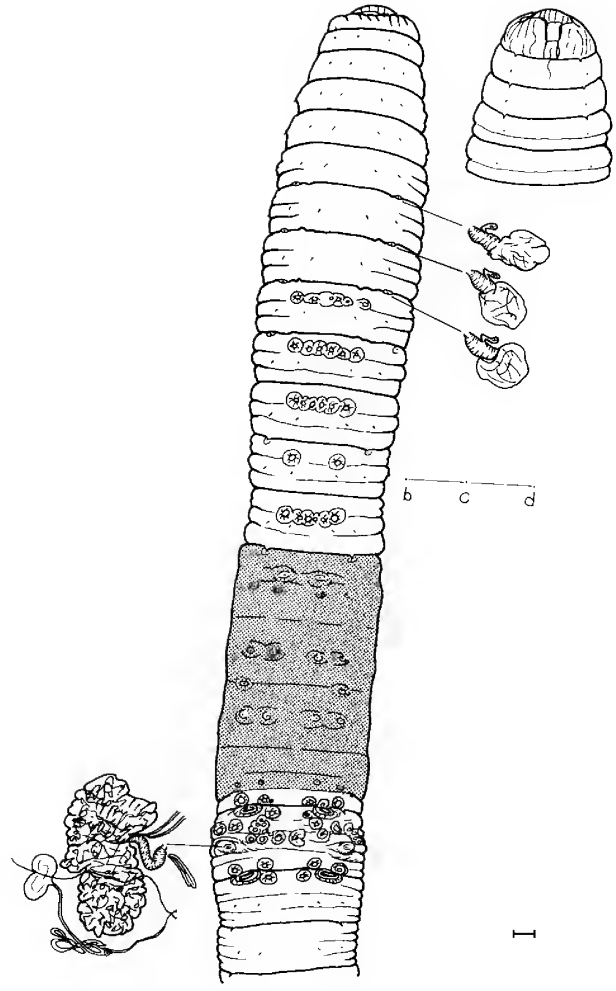

Figure 13. *Heteroporodrilus narrabri* n.sp., ventral view of holotype with dorsal view of tanylobous prostomium; spermathecae *in situ*; and lhs prostate in 18–19 with vasa deferentia and long penial setae; nephridial bladder of 19 lhs is also shown on septum. Scale 1 mm.

Remarks. *Heteroporodrilus narrabri*, with four pairs of calciferous glands and three pairs of spermathecae is similar to several other species in the genus. It differs from *H. mediterreus* principally by having seminal vesicles in 9 and 12 (rather than 11 and 12); from *H. canaliculatus* by having single spermathecal diverticula mid-length on the duct (rather than paired or multiple and near the exit); from *H. shephardi* by having prostate glands that are not clearly divided into two lobes; and from *H. namoi* by having diverticula near the mid-length of the spermathecal duct (rather than near the exit). From all four species, *H. narrabri* differs further by the more dorsal commencement of its dorsal pores in 11/12 (rather than in 5/6, 6/7, or 8/9) and in the complex arrangement of its genital markings.

Nevertheless, *H. narrabri* is remarkably similar to both *H. shephardi* and *H. namoi* as described herein, especially with regards the primary genital markings. These markings comprise two pairs of sucker-like pads in *ab* lines anteriorly on 18 and 19 (as in *H. shephardi*) as well as a tendency to

smaller more numerous ancillary markings (as seen in *H. namoi*). Also similar in these three species are nephropore shifts between *d* to both mid-*bc* and *c* lines in some anterior segments (it is also possible this arrangement occurs in *H. mediterreus* as some nephropores could not be clearly determined). This alternation of nephropores from *d* to mid-*bc* was once thought (Jamieson, 1974b: 87) to be unique for *H. shephardi*—this assumption is further questioned in the remarks under the description of the latter species below.

Etymology. Named after the locality.

Distribution and habitat. Narrabri in northern central NSW, sits astride the River Namoi that, flowing approximately 200 km westwards to Walgett (the type locality of *H. namoi*), joins the Barwon River that passes through Brewarrina uniting with the Darling River near Bourke (both latter localities forming the known range of *H. mediterreus*). Trangie and Warren, are adjacent townships on the Macquarie River that also flows to the Darling. The Murray-Darling River system leads eventually to Vic./SA where *H. hirthi* and *H. shephardi* are found.

Habitat details for these specimens (provided by the collector) are from a 2.1 ha field of raised bed rows of lucerne and cotton at the Australian Cotton Research Institute (ACRI). This field (B16) was managed without insecticides and with minimum tillage for 3 years (previously under conventional cotton i.e., sprayed and irrigated for 15–20 years), indicating that this species can recolonize or persist under such management regimes.

Heteroporodrilus shephardi (Spencer, 1900)

Figs. 14, 20

Cryptodrilus shephardi Spencer, 1900: 40–41, figs. 28–30; Jensz & Smith, 1969: 91.
Woodwardia shephardi.–Michaelsen, 1907: 162.
Heteroporodrilus shephardi.–Jamieson, 1970: 122–124, figs. 4c–d,9f,10i; Blakemore, 1994b: 21–23.
Heteroporodrilus shephardi (Spencer, 1900) *armatus* Jamieson, 1974b: 85–87, figs. 2b, 10b, 11a, 13; **new synonym**.

Material examined. Spencer specimen: AM W1290, part of Fletcher Collection donated to Australian Museum. Sample contains four labels: "C. sp 1aV W Dimboola D. le Souëf" [Species code, location and collector in Spencer's handwriting]; "*Cryptodrilus* sp 1a Nr Dimboola, Vict[oria] W.1290" [Fletcher's writing?]; "*H. shephardi* Coll by J.J. Fletcher (Prof B. Spencer *fide* Fletcher) re-identified by Dr B Jamieson 1970"; "W.1290 *Heteroporodrilus shephardi* Nr. Dimboola Vic. Id. E. Easton". (Specimen mature clitellate, previously partially dissected in midbody—it agrees with this taxon being 140 mm long, with markings in 10–12 and 18 & 19 and has large penial setae). This specimen is clearly identified with specimen NMV G74 missing from the Museum of Victoria Spencer Collection (Jensz & Smith, 1969: 91). However, it is not part of the type-series as, in his type description, Spencer does not refer to this locality (Dimboola is approximately 35 km northwest of the Horsham type-locality) nor to this collector (here identified as Mr Dudley Le Souëf, rather than Mr J. Shephard). Specimens: (S1) ANIC RB.98.8.1, Victor Harbour, S.A., collected by C. Davoren, 23.viii.1991, "in vegy garden" (mature specimen, relaxed on preservation, dissected and figured here). (S2) SAM E3033, same details as S1, (mature specimen, contracted on preservation, dissected).

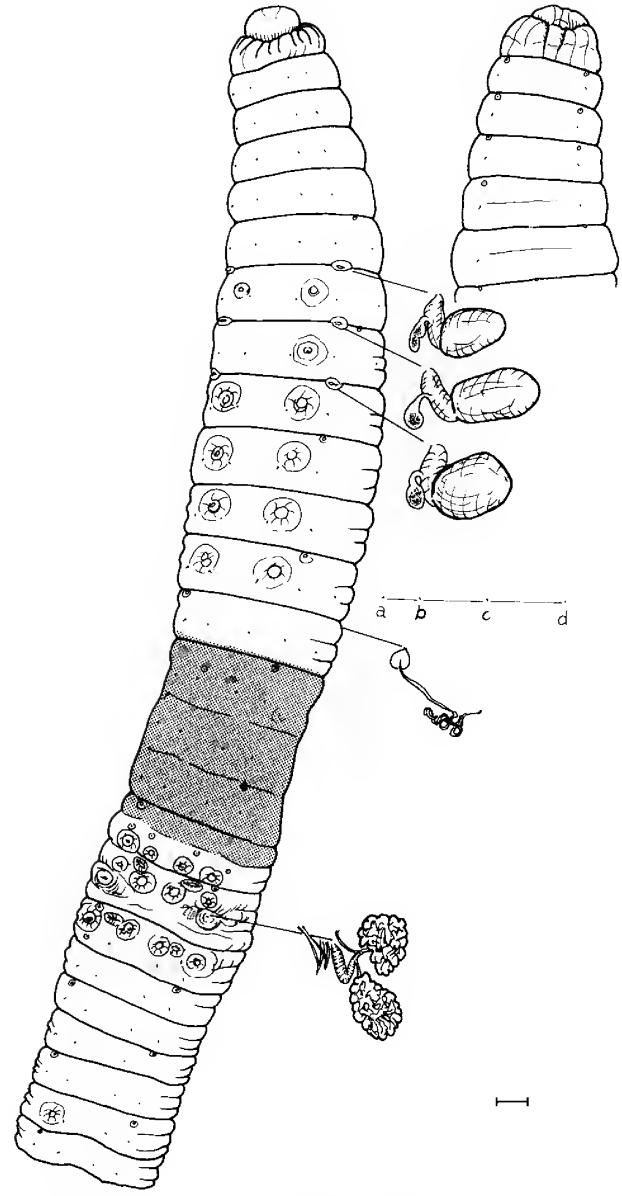

Figure 14. *Heteroporodrilus shephardi* (Spencer, 1900), ventral view of Victor Harbour specimen with dorsal view of prostomium; spermathecae; nephridial bladder in 13 rhs; and bilobed prostate in 18–19 with vasa deferentia and penial setae. Scale 1 mm.

Type material not re-examined here. LECTOTYPE: NMV G34, a dissected entire specimen, in reasonable condition from Horsham, Vic., collected by Mr J. Shephard in October, 1892 (Jensz & Smith, 1969: 91). Paralectotypes: NMV G1409, two complete specimens formerly included with G34. (One of these was examined and figured by Jamieson [1970], although he makes no mention neither of the lectotype, the other paralectotype, nor the AM specimen he apparently re-identified).

External features. Body not dorsally canaliculate. Lengths, mm: 170 (S1), 90 (S2), c. 157–160 (Spencer, 1900; Jensz & Smith, 1969), 112 (Jamieson, 1970). Width: c. 5 mm (S1, S2 and Spencer) (cf. 10 mm, Jamieson, 1970—but in his figs. 4c,d the scale bars are obviously wrong). Segments:

103 (S1), 100 (S2). Colour: (new material) dorsum to *d* lines gunmetal grey, with darker spinal line, flanks between *dc* lighter grey, ventrum pale; clitellum buff. Prostomium: epi-tanylobous (possibly pro-epilobous). Clitellum: weak ¼13–½17. Dorsal pores: 5/6 minute in (S1), open from 6/7 (S1, S2 and Spencer). Setae: 8 per segment in regular series. Nephropores: (in S1): at anterior margin of segment in *d* lines in 2–4, and on 5 rhs, 6 lhs, 7 rhs, 8 lhs, 9 rhs, 10 lhs, then on alternate segments; in mid-*bc* lines on 5 lhs, 6 rhs, 7 lhs, 8 rhs, 9 lhs; in *b* lines on 10 rhs, then on alternate segments; (in S2): alternations are same except on opposite sides and on 5 lhs only in *c* line; (cf. lectotype, Jamieson, 1970: in *d* lines in 2–4, 7 rhs, 8 lhs, 9 rhs; in *c* lines on 5–6 rhs; in mid-*bc* on 5–6 lhs, 7 lhs, 8 rhs, 9 lhs; then alternating in *b* and *d* lines). Spermathecal pores: 6/7/8/9 in setal *b* lines. Female pores: paired just anteromedian to setae *a* on 14. Male pores: paired near *b* lines on small papillae on 18 (S1) or on prominent mounds (S2). Genital markings: inconspicuous mostly paired discs, just anterior to *ab* in 7,8–12,13; in 17 two pairs of postsetal discs, just median to *b* and *a* lines (S1) or just the latter pair visible (S2); in 18 two pairs of presetal discs, just median to *b* and *a* lines (S1, W1290) or just the latter pair (S2), with small intervening sucker-like pad closer to intersegmental furrow on each side; in 19 two pairs of presetal discs, one pair just lateral to *b* lines, one pair median to *a* lines with small intervening sucker-like pad on each side; weak lhs analogue of disc in *ab* on 24 (in S1 only). Anterior markings difficult to see without adequate side-lighting; the male field in S2 in deep depression with the male pores on prominent mounds and only marking and pads (or pits) on 18 and 19 clearly visible (as Spencer).

Internal anatomy. Septa: 5/6–12/13 increasingly thickened, then thin. Gizzard: muscular barrel-shaped in 5. Oesophagus: small ventrolaterally sessile calciferous glands paired in 10–13 (i.e., four pairs). Nephridia: vesiculate holoic with small spherical bladders in position of nephropores. Vascularization: dorsal blood vessel single; hearts paired in 10–13 with connectives to supra-oesophageal vessel in 9–13. Spermathecae: three pairs in 7–9, large ampulla on moderately thick duct mid-length on which is small clavate diverticulum. Male organs: holandric, iridescent testes and funnels in 10 and 11 in mucus; seminal vesicles paired, racemose in 9 and 12. Ovaries: as sheets of numerous minute egg-strings in 13; small paired ovisacs in 14. Prostates: bilobed, racemose in 18–19 (S1) or 17–20 (S2); fine penial setae with attached muscle fibres present (S1, S2). Intestine: origin in 15 (S1 and Spencer) or ½15 (S2); no typhlosole; gut contains dark organic soil.

Remarks. The present specimens agree with Spencer's characterization of *H. shephardi* on almost every given point. Especially similar are the prostomium (described by Spencer as "scarcely at all dovetailed into the peristomium"), the arrangement of the alimentary canal (i.e., with four pairs of calciferous glands in 10–13 and intestinal origin in 15), the position of the seminal vesicles (in 9 and 12) and the bilobed prostates. Moreover, the male field with deep depression in 17 and 18 and with paired markings anteriorly in 18 and 19 (as described and figured by Spencer) corresponds to that of the contracted specimen, S2, while more extensive markings are visible on the less contracted S1. A questionable difference is that Spencer (1900) described the spermathecae as "consisting of a spherical sac with a long duct into the base of which [rather than into the mid-length as here] opens a short tubular diverticulum with a slightly swollen end." However, in Spencer's fig. 30, at least one spermatheca is shown with the diverticulum further from the base. While agreeing in general shape, the diverticula here open mid-length on the duct and are similar to that of a paralectotype figured by Jamieson (1970: 141, fig. 10i).

Jamieson (1970), in his redescription of one of the paralectotypes, reported more extensive genital markings than Spencer, including inconspicuous anterior markings in 8–11 and postsetal markings in 17 (as in S1 and S2 here). He was unable to detect the anterior markings in 18 and 19 (as Spencer, 1900 and also as in present account).

The distinction of a sub-species, proposed by Jamieson (1974b) as "*Heteroporodrilus shephardi* (Spencer, 1900) *armatus*" for four or five specimens from south of Bordertown in S.A., is here questioned. Jamieson (1974b: 87) justified his sub-species on the grounds of its having detectable penial setae and slight differences in genital markings. Yet some ambiguity remains about penial setae in *H. shephardi*, since Jamieson (1970: 123) stated that "setae *a* visible immediately median" to the male porophores then asserted "Penial setae absent" from paralectotype NMV G1409. In his "descriptive notices", Spencer (1900) rarely recorded presence or absence of penial setae, and whether they actually occur in the lectotype NMV G34 is undetermined (a task beyond the scope of the present study). Moreover, new material here agreeing with Spencer's species do have penial setae, as well as variations in genital markings that encompass those of earlier descriptions of both "sub-species" (perhaps accounted for by artefacts of preservation, to observational conditions, or to ontological state of the specimens). Jamieson's sub-species is therefore synonymised with *H. shephardi*; a questionable difference remaining is the exact position of the diverticulum on the spermathecal duct (cf. Spencer, 1900: fig. 30 and Jamieson, 1970: 141, fig. 10[i] and Jamieson, 1974b: 107, fig. 10b).

When justifying his sub-species, Jamieson (1974b: 87) stated "The new material agrees with *H. shephardi* alone in the genus (*vide* Jamieson, 1970) in alternation of nephropores between *d* and mid *bc*, rather than the usual *d* to *c*" and went on to assert "it is unquestionably, from its morphology, more closely related to the latter than to any other taxon in *Heteroporodrilus*." However, this is not supported by the evidence on viewing Jamieson (1970: 122 and 117) where his redescription of the *H. shephardi* lectotype has nephropores in 5–9 in mid-*bc* or in *c* lines, and his redescription of *H. mediterreus* has nephropores "not determinable" in 7–9. Moreover, nephropores intermittently in this location have been noted for several other species newly described here.

Distribution and habitat. Specimen W1290 was from the Mallee district in Dimboola, Victoria (Jensz & Smith, 1969: 91). Dimboola, on the Wimmera River upstream from Horsham, is the type-locality of *Anisochaeta notabilis* and *Megascolides diaphanus* (Spencer, 1900 both). For the latter

species from West Dimboola, Spencer (1900) remarked that "The Flats [close to the River Wimmera] on which the worm was found are liable to be flooded at rainy seasons but are at other times perfectly dry". Victor Harbour, near the mouth of the River Murray, is approximately 400 km west of the Horsham, Vic. type-locality. Jamieson's specimens were collected from a region intermediate between Horsham and Victor Harbour, near the SA/Vic. border.

Heteroporodrilus shephardi appears more closely related to several *Heteroporodrilus* species known from floodplains of central NSW, especially *H. mediterreus, H. namoi*, and *H. narrabri*. Such wide distribution of closely related forms is unusual for most native taxa, and can be attributed to fluvial transportation and migrations along connected waterways of the Murray-Darling (see Fig. 20 for present day river system).

Genus *Cryptodrilus* Fletcher

Cryptodrilus Fletcher, 1886: 570; Jamieson, 1972: 154–155, 1974a: 266; Blakemore, 1997a: 1687–1688.
Trinephrus Beddard, 1895: 483.

Diagnosis. Setae 8 per segment. Dorsal pores present or absent. Male pores from tubuloracemose or racemose prostates paired on 18. An oesophageal gizzard in 5. Nephridia vesiculate meroic, with multiple bladders in at least some segments of body. Spermathecae two (or three) pairs, with one or more clavate diverticula. Extramural calciferous glands and typhlosole absent or present; intestinal caeca absent. Penial setae present or absent.

Type species. *Cryptodrilus rusticus* Fletcher, 1886: 570–573 from Burrawang, NSW. (Syntypes, AM W1389).

Included species

Cryptodrilus dubius Spencer, 1892: 136–137, figs. 13–15, 67, from Victoria probably Croajingolong, East Gippsland. (Lectotype NMV G35).
Cryptodrilus fastigatus Fletcher, 1889, from Burrawang, Illawarra, Bega-Bombala, and Mt Kosciuszko, NSW. (Types AM W1308).
Cryptodrilus mediocris Fletcher, 1889: 1544–1546, from Newington, near Parramatta, NSW. (Syntypes AM W1313).
Cryptodrilus naroomai n.sp. from Narooma, NSW.
Cryptodrilus polynephricus Spencer, 1895: 35–36, figs. 4–6, from Mt. Wellington and Parattah, Tasmania. (Type material NMV G1436—not found, possibly on loan).
Cryptodrilus rusticus Spencer, 1892, from Victoria.

Five additional species from Tasmania are currently in the process of description (Blakemore, in prep.). The status of several taxa previously attributed to *Cryptodrilus* is uncertain as the presence or absence of nephridial bladders has not been satisfactorily determined.

Distribution. Southern New South Wales, Victoria, Tasmania.

Remarks. The most recent discussion of this genus is by Blakemore (1997a). The generic diagnosis is changed slightly to include species with extramural calciferous glands as are found in a taxon newly described below. Only the presence of nephridial bladders now distinguishes *Cryptodrilus* from *Notoscolex* (although the multiloculate spermathecal diverticula of the type species of the latter genus are possibly significant).

Cryptodrilus fastigatus Fletcher, 1889

Fig. 15

Cryptodrilus fastigatus Fletcher, 1889: 1541–1543; Jamieson, 1972: 161–166, figs. 5AB, 6AB, 7A; 1973: 229–233, fig. 3.
Trinephrus fastigatus.–Beddard, 1895: 483; Michaelsen, 1900: 185.
Notoscolex fastigatus.–Michaelsen, 1907: 162.

Material examined. Specimens: AM W24420 (S1), Fred Piper Lookout, Bega-Bombala region, NSW, c. 36°41'S 149°51'E, Ed Easton, 1.vi.1983, "Jar 75 Sp 41", "Octochaetine sp., dark red", (complete mature, figured and dissected); ANIC RB.98.2.12, (S2) same details, (mature specimen, posterior amputee, dissected and figured). Type material not re-examined here. AM W1308, labelled in Fletcher's hand "*Cryptodrilus* Bg. and Illawarra".

Fletcher based his description on "Five spirit specimens" from "Burrawang, and Illawarra, NSW"; six clitellate specimens were re-examined by Jamieson (1972): One was designated the lectotype; four others being designated paralectotypes (total 5?); though two of the type series (total 7?), supposedly from Burrawang, were not regarded as types by Jamieson (1972: 166) as details of their male fields differed slightly from that of the Illawarra specimen—see Remarks below.

External features (compared with type description). Body widest before clitellum, tapering steadily after clitellum. Lengths, mm: 85 (S1), 50+ (S2), 63–89 (Fletcher). Width: 2–3 mm. Segments: 158 (S1), c. 100–140 (Fletcher). Colour: "dark red" in life; anterior dorsum dark grey otherwise pale in alcohol; clitellum brick red, ("above reddish or purplish tinged with brown, or iridescent purplish, lighter below"—Fletcher). Prostomium: widely tanylobous; peristomium ventrally cleft. Clitellum: 14–17 with slight canal dorsally. Dorsal pores: from 4/5, larger from 5/6 (S2 and Fletcher, in S1 the dorsal pores commence from 6/7 but it is possible that there is some anterior anomaly as some setae and nephropores are missing from the first six segments). Setae: 8 per segment in regular series. Nephropores: conspicuous at anterior margin of segments in *a, c* and *d* lines in all segments except some around the male field (see Remarks below). Spermathecal pores: two pairs in 7/8/9 in *a* setal lines (just anterior to nephropores). Female pores: widely paired immediately anteromedian to *a* setae on 14. Male pores: paired at centres of low mounds approximately in *ab* lines on 18. Genital markings: only as indistinct tumid areas, differing variously between specimens, e.g., ill-defined ventral tumidity in 7–9 and 17–19,20 in S1 and S2. (Paired or single midventral pore-like "markings" around the male field are just that, nephropores—see description of Nephridia, and Remarks below).

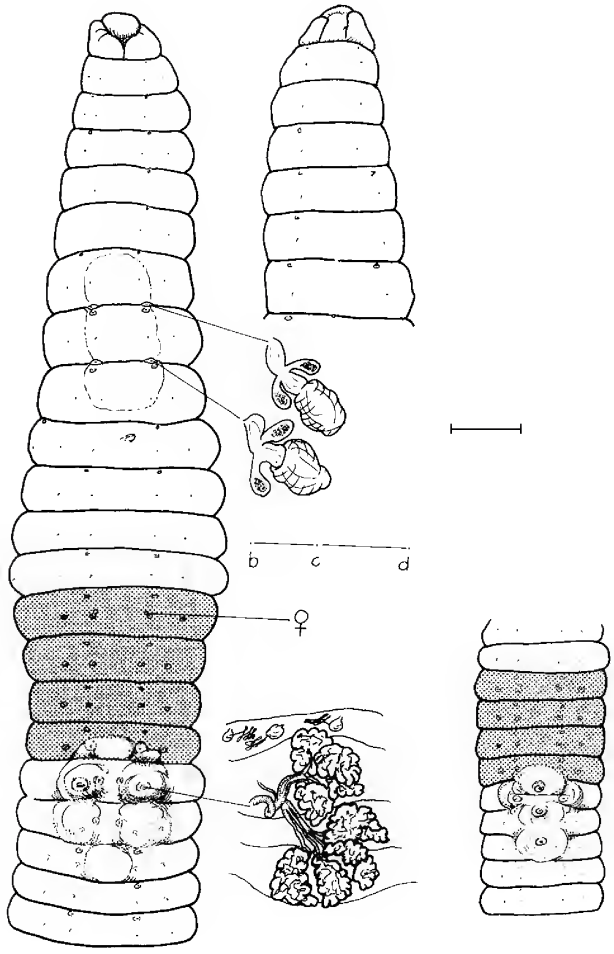

Figure 15. *Cryptodrilus fastigatus* Fletcher, 1889, ventral view of Bega specimen (S1) with dorsal view of prostomium; spermathecae; nephridial arrangement in 17 preceding the multilobed racemose rhs prostate in 18–20; also shown is male field of second specimen (S2) for comparison. Scale 1 mm.

Internal anatomy. Septa: none especially thickened except perhaps 11/12/13. Gizzard: muscular in 5, slight and barely wider than oesophagus. Oesophagus: dilated but thin walled in 12–13, then increasingly dilated and vascularized in 14–16 with internal lamellae possibly forming rudimentary annular calciferous glands; valvular in 17. Nephridia: vesiculate meroic with three sets of tubules per side, each with small spherical bladder in *a, c* and *d* lines; not tufted in anterior. (In S1 nephropores from setal *a* lines are displaced ventrally and posteriorly to occur median of setal *a* lines in 18 and 19; while in S2 they combine mid-ventrally as single pores in 18–20. As nephridial bladders are retained in setal *a* lines as usual in these segments, it is surmised that the ducts are extended and displaced after they enter the body wall). Vascularization: dorsal blood vessel single onto pharyngeal mass in 4–5; hearts increasingly large in 10–12 from weak supra-oesophageal vessel (Fletcher states last hearts "in 12 [in one specimen but in 13 in another]."). Spermathecae: two pairs in 8–9, pouch-like ampulla on thick duct with small pair of opposed club-shaped diverticula mid-length. Male organs: holandric, iridescent testes and funnels in 10 and 11; seminal vesicles paired, racemose anteriorly in 11 and 12. Ovaries: large palmate with numerous oocytes in 13; small ovisacs in 14. Prostates: massive, three-dimensional highly racemose bodies with externally branching ducts in 18–20; penial setae absent. Intestine: origin in 18; typhlosole absent; gut contains organic material and gritty soil particles.

Remarks. The above specimens are darkly pigmented (as noted on Easton's label), on this, and on all other points, they concur with each other and with Fletcher's type description.

Jamieson (1972, 1973) went to some length describing and attempting to interpret the variations in the "genital markings" configuration around the male field in the type material, as well as in specimens from Mt Kosciuszko. Jamieson (1973: 230–233, 248) concluded that "The unparalleled diversity in the male genital field in *C. fastigatus* on Mt Kosciusko, which exceeds variation known in any other oligochaetes, merits further investigation. Possibly polytypic variation between isolates segregated by ice flows from the former cap glacier has survived as intra-population polymorphism following introgression of the former isolates."

However, the pore-like "genital markings" occurring variously around the male field and clitellum are here interpreted as irregularly displaced nephropores, that form tumescences for undetermined physiological reasons (such as the "nephridial packing problem" or physical dislocation due to the development of the prostate glands, oesophageal dilations and clitellum in these segments). The reasoning for this conclusion are:

1 Nephropores are not found in setal *a* lines in segments where these displaced pores occur (although internally the nephridial bladders retain their normal setal *a* line position and presumably these still function for excretion via pores).
2 Where the nephropores are in their usual position outside the male field, they sometimes develop paired or unilateral tumescences.
3 Although the body wall in the region of these pores is thickened, no corresponding glandular structures are found on the internal surfaces.
4 Actual pores associated with genital markings occur rarely in megascolecids.
5 Attribution of these pores to excretion, rather than to copulation, would account for their intraspecific variability and remove the need for complex explanations of compatibility. (Notwithstanding this interpretation of their nature as excretory, the secretion from these nephropores may yet have some secondary role in copulation).

In view of this conclusion, the slight differences in the "male genital fields" of the two Burrawang type specimens does not exclude them from this taxon and, as they formed part of the type description, they must be syntypes.

Spencer (1892: 137) considered his *Cryptodrilus dubius* from Victoria (probably from Croajingolong) to be closely

allied to *C. fastigatus*, except for its well developed calciferous glands in 15 and 16. Separate specific status of *Cryptodrilus dubius* is maintained on the basis of this character.

Distribution and habitat. The type-localities are Burrawang and the nearby Illawarra district of NSW; also found in the Bega-Bombala region and from Mt Kosciuszko.

Cryptodrilus naroomai n.sp.

Fig. 16

Material examined. HOLOTYPE: AM W24454 (H), Narooma/ Bega Rd, NSW, c. 36°30'S 149°50'E, Ed Easton, 1.vi.1983, "Jar 74 Sp 36", "[illegible] km N of B", "Octochaetine [8 setae] colourless", (complete mature, figured and dissected). PARATYPES: all same details as (H), ANIC RB.98.2.18, (P1), (mature, dissected and figured); W24455, (P2), (clitellate mature, dissected); ANIC RB.98.2.19, (P3), (aclitellate mature, dissected); AM W24456 (P4–P17), sample in original jar (14 specimens, 9 aclitellate matures or subadults and 5 juveniles that superficially agree having various combinations of nephropore distributions around male fields).

External features. Body slender. Lengths, mm: 130 (H), 88 (P1), 70 (P2), 105 (P3). Width: c. 4 mm. Segments: 180 (H), 175 (P1). Colour: unpigmented; clitellum puce. Prostomium: widely tanylobous; peristomium ventrally cleft. Clitellum: 14–17. Dorsal pores: from 4/5 (H, P1), larger from 5/6 (P2, P3). Setae: 8 per segment in regular series. Nephropores: conspicuous at anterior margin of segments in *a, c* and *d* lines in all segments from 3 except some around the male field: in (H) they form tumescences in *a* lines on 16 lhs and 17 lhs and are (combined) mid-ventral on 18; in (P1) they are displace to lateral of *b* lines at anterior of 18 within large pads. Spermathecal pores: two pairs in 7/8/9 in *a* setal lines (just anterior to nephropores). Female pores: widely paired immediately anteromedian to *a* setae on 14. Male pores: paired at centres of low mounds approximately in *a* lines on 18. Genital markings: only as indistinct tumid areas; in (H) 9 and 18 are tumid ventrally; (P1, P2, P3) have swelling around male pores.

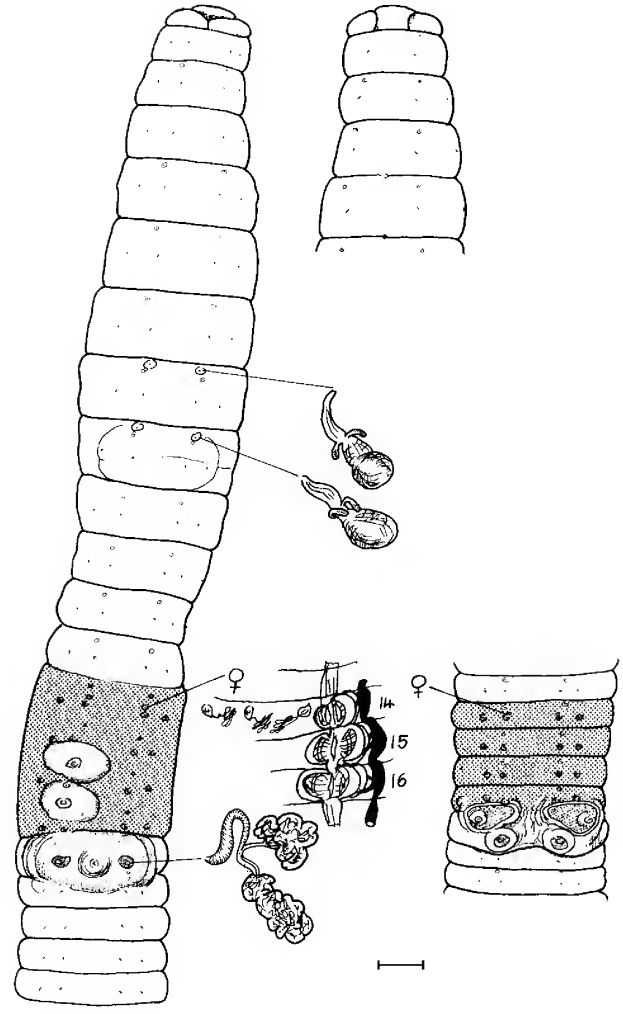

Figure 16. *Cryptodrilus naroomai* n.sp., ventral view of holotype with dorsal view of tanylobous prostomium; spermathecae; section through calciferous glands in 14–16, also showing nephridial arrangement in 14; and bilobed rhs prostate in 18–19; male field of specimen (P1) is shown for comparison. Scale 1 mm.

Internal anatomy. Septa: 8/9–12/13 slightly thickened. Gizzard: large conical in 5, displaced to occupy segments 7–9. Oesophagus: with increasingly large paired lateral pouches in 14–16 (i.e., three pairs of extramural calciferous glands) supplied by capillary branches from dorsal vessel, with closely packed internal lamellae; narrows 17–½18. Nephridia: vesiculate meroic with three spherical bladder in *a, c* and *d* lines, some appear to have more than one set of tubules attaching to bladder; in (H) bladder in *a* line in 18 lhs goes to body wall; small tufts in 2–4. Vascularization: dorsal blood vessel single; hearts 10–12 from supra-oesophageal vessel in 10–14. Spermathecae: two pairs in 8–9, pouch-like ampulla on thick duct with small pair of opposed club-shaped diverticula mid-length. Male organs: holandric, iridescent testes and funnels in 10 and 11; seminal vesicles paired, racemose anteriorly in 11 and 12. Ovaries: large palmate with sheets of long egg-strings in 13; small ovisacs in 14. Prostates: racemose, divided into two lobes with externally branching ducts in 18–19; penial setae absent. Intestine: origin ½18; typhlosole absent; spiralling gut contains loamy soil with charcoal and large sand grains.

Remarks. Morphological differences of *Cryptodrilus naroomai* from *C. fastigatus* are the larger somatic size, lack of pigmentation (see Easton's labels); a larger gizzard, and three pairs of extramural calciferous glands in 14–16. *Cryptodrilus naroomai* is also larger than *C. dubius* and has extramural calciferous glands in 14 in addition to 15 and 16. The lack of pigmentation and more developed digestive system (and the contents of the gut) suggest a different ecological strategy compared to the sympatric *C. fastigatus*. Determination of specific status depends on inferred behavioural differences conferring reproductive isolation and morphological variation.

The variations in positions of the nephropores around the male fields and their papillation on the clitella confirms the conclusions made for *C. fastigatus* above, that their primary function is excretory, rather than for mate recognition and copulation.

Etymology. Named after the type locality.

Distribution and habitat. Narooma is about 60 km north of Bega on coastal southern NSW and within the distributional range of *C. fastigatus*.

Genus *Notoscolex* Fletcher

Notoscolex Fletcher, 1886: 546; Michaelsen, 1900: 187; 1907: 160–162; Stephenson, 1930: 836; Lee, 1959: 317; Gates, 1959: 254; Jamieson, 1973: 235; Blakemore, 1997a: 1688–1689.
Tokea Benham, 1904: 240.
Pseudonotoscolex Jamieson, 1971: 496.
Oreoscolex Jamieson, 1973: 238; 1974a: 302; **new synonym**.

Diagnosis. Setae 8 per segment. Dorsal pores present or absent. Male pores from racemose or tubuloracemose prostates paired on 18. An oesophageal gizzard in 5 or 6. Nephridia meroic, at least in the fore-body, avesiculate, sometimes tufted. Spermathecae two or three pairs (or unpaired, typically with multiloculate sessile or one or more clavate diverticula. Typhlosole typically absent; extramural calciferous glands typically present; intestinal caeca absent. Penial setae typically present.

Type species. *Notoscolex camdenensis* Fletcher, 1886: 546–551, Pl. VII, figs. 1–5, from Burrawang, NSW. (Syntypes NMV G170).

Included species

About seventy species are placed in this genus, including several transferred from *Cryptodrilus, Oreoscolex* and *Pseudonotoscolex*. Many described *Notoscolex* species require confirmation of lack of nephridial bladders to qualify for inclusion, a task beyond the scope of the current study.

Distribution. New South Wales, Victoria, Tasmania, Western Australia, southern Queensland, New Zealand, (?South India, Sri Lanka). Gates (1972: 132) questions whether any Indian species actually belong in this genus.

Remarks. The most recent treatment of this genus is by Blakemore (1997a). As unpaired spermathecae are unlikely to be of more than specific value (see Gates, 1972: 132), *Oreoscolex* is synonymized in *Notoscolex*. Jamieson (1974: 266, 302) had expanded the definitions of *Cryptodrilus* and *Oreoscolex* so that they were not mutually exclusive and, moreover, subsumed the characters of the prior genera *Megascolides* and *Notoscolex*. The two new species added here do not require substantial change to the generic diagnosis, although it should perhaps be noted that one species has six pairs of extramural calciferous glands (in segments 8–13), and has large tubuloracemose prostates, but lacks penial setae. The separation of *Cryptodrilus* from *Notoscolex* is thus reinforced on a single character state: vesiculate meroic in *Cryptodrilus* vs. avesiculate meroic in *Notoscolex*.

Notoscolex harenapascuus n.sp.

Fig. 17

Material examined. HOLOTYPE: AM W24423 (H), Muogamarra Nature Reserve, Berowa/Brooklyn Road, NSW, c. 33°38'S 151°12'E, Ed Easton, 6.vi.1983, "Jar 82 Sp 10", "Octochaetine colourless sp", (complete mature, figured and dissected). PARATYPES: all same details as (H), ANIC RB.98.2.13, (P1), (aclitellate mature, dissected); W24424, (P2), (aclitellate mature); ANIC RB.98.2.14, (P3), (aclitellate mature, posterior amputee); AM W24425 (P4), (subadult); AM W24426 (2 immatures that agree superficially plus a tail portion).

External features. Body circular in section. Lengths, mm: 95 (H), 100 (P1), 80–85 (P2, P4). Width: c. 5 mm. Segments: 183 (H), 199 (P1). Colour: beige in alcohol; clitellum orange. Prostomium: short closed epilobous. Clitellum: ½13–17. Dorsal pores: from 9/10. Setae: 8 per segment *ab* deleted on 18, *d* lines sinuous in posterior. Nephropores: not found. Spermathecal pores: two pairs in 7/8/9 just lateral of setal *a* lines. Female pores: widely paired on 14. Male pores: paired on summits of large mounds in *b* on 18. Genital markings: large mid-ventral pads in *aa* lines in 13/14/15/16 (H) or 13/14–16/17 (P1–P3) and 21/22 (H) or 22/23 (P1), with pore-like dimples that are variously single, paired, triad or tetrad; ventral aspect of 18 occupied by waisted pad between male porophores that also has tetrad dimples (H-P4).

Internal anatomy. Septa: 5/6 thin to base of gizzard, 6/7–10/11 increasingly thick. Gizzard: large thick walled and muscular in 5. Oesophagus: large laterally paired reniform calciferous glands in 8–13 (i.e., six pairs), attach to gut by short ducts, with numerous internal lamellae and white granules, well supplied by blood vessels; narrowing in 14–15. Nephridia: avesiculate meroic with several tubules (c. 8 per side) equatorial but attaching to anterior septa; tufted in (4)-5. Vascularization: dorsal blood vessel single; hearts 10–13; weak supra-oesophageal vessel present supplying calciferous glands. Spermathecae: two pairs in 8–9, flattened saccular ampulla on tapering duct with curt or sessile, multiloculate diverticulum towards junction. Male organs: holandric, iridescent testes and funnels in 10 and 11; seminal vesicles paired, racemose anteriorly in 11 and 12. Ovaries: (not located); small ovisacs in 14. Prostates: large deeply-lobulated tubuloracemose glands in 18–27 on short coiling ducts; penial setae not found. Intestine: origin in 16; typhlosole absent; gizzard and intestine full of quartz grits and grey colloidal soil.

Remarks. The intersegmental genital markings and male field are distinctive in *Notoscolex harenapascuus*. Multiloculate, sessile diverticula on the spermathecae, and

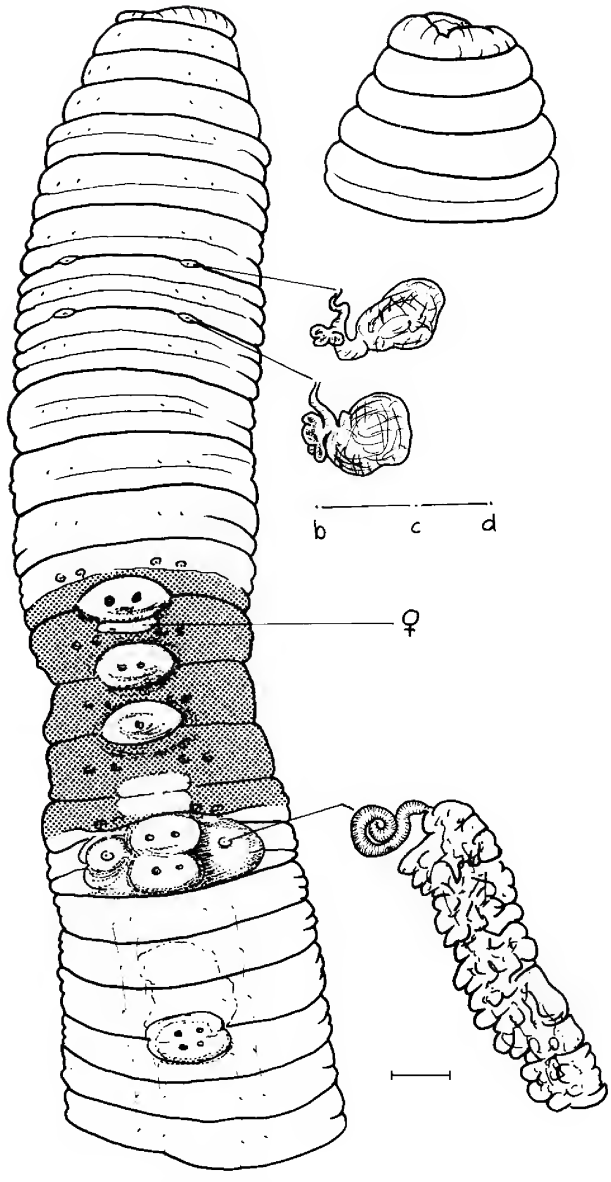

Figure 17. *Notoscolex harenapascuus* n.sp., ventral view of holotype with dorsal view of prostomium; spermathecae; and rhs tubuloracemose prostate in 18–27. Scale 1 mm.

well developed, extramural calciferous glands are additional features that are shared with the type species, *N. camdenensis* which, however, has only three pairs of these glands in 14–16 (rather than six pairs in 8–13) and prostates that are racemose (rather than elongate tubuloracemose as here). Other characteristics of *N. harenapascuus* are seminal vesicles in 11 and 12, and the last hearts in 13.

Etymology. The word combination *harena-pascuus* (Latin) means grit-grazing and refers to the gut contents.

Distribution and habitat. Berowa north of Sydney, NSW.

Notoscolex meekae n.sp.

Fig. 18

Material examined. HOLOTYPE: ANIC RB.98.6.1 (H), Big Jack Mountain Rd., Rocky Hall, Wyndham, southeastern NSW, 36°52'30"S 149°30'E, Heather Meek, 5.i.1998, (complete mature, figured and dissected). PARATYPES: none.

External features. Body stout. Length, mm: 360 (extends up to 500 mm in life). Width: c. 5 mm. Segments: 225. Colour: in life pale olive; in alcohol uniform grey with darker mid-dorsal line and clitellum. Prostomium: short pro-epilobous. Clitellum: 14–½19 (14–17 ventrally). Dorsal pores: from 3/4, occluded on clitellum. Setae: 8 per segment, *ab* absent from 18, *d* lines slightly sinuous in posterior. Nephropores: not found. Spermathecal pores: four pairs at posterior border of segments 5–8 (i.e., almost in 5/6–8/9) just lateral of setal *a* lines. Female pores: widely paired on 14. Male pores: superficial in *ab* lines at lateral points of diamond-shaped pad within paired parentheses occupying

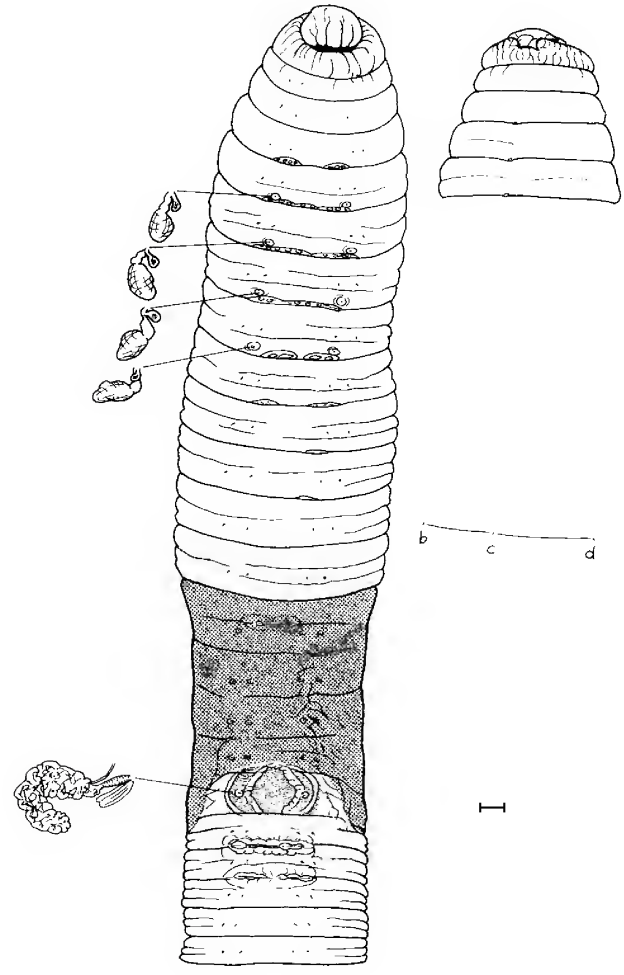

Figure 18. *Notoscolex meekae* n.sp., ventral view of holotype with dorsal view of epilobous prostomium; spermathecae; and lhs prostate with vasa deferentia and penial setae in 18. Scale 1 mm.

whole ventral aspect of 18 as wide as *b* lines. Genital markings: barely perceptible paired elongate markings seen ventrally in intersegments 4/5–9/10/11/12; more defined elongate tumid pads in *bb* in 19/20 and 20/21.

Internal anatomy. Septa: 7/8–12/13 increasingly thick. Gizzard: muscular barrel in 5. Oesophagus: not especially dilated; valval in 16. Nephridia: avesiculate meroic, large forests of tubules in 3–4, smaller in 5 from whence they spread equatorially in wide band with c. 50 tubules per side; no preseptal funnels found. Vascularization: dorsal blood vessel segmentally doubled (recombining at septa) from 5; hearts 10–13 from supra-oesophageal vessel in 9–13,14. Spermathecae: four pairs in 6–9, saccular ampulla on shorter duct with small clavate diverticulum ectally. Male organs: metandric, iridescent testes and funnels in 11 only; seminal vesicles paired, racemose anteriorly in 12 only. Ovaries: compact egg-strings in 13; small ovisacs in 14. Prostates: tubuloracemose glands in 18 on short ducts; penial setae as long as duct. Intestine: origin in 17; typhlosole absent; gut contains fine organic soil.

Remarks. Distinctive features of *Notoscolex meekae* are its large size, the four pairs of spermathecal pores at the posterior borders of segments 5–8, the doubled dorsal blood vessel, metandric male organs, and the distribution of the genital markings.

Etymology. Named after the collector.

Distribution and habitat. Rocky Hall is situated amidst the NSW Southeast State Forests. This specimens was collected from bushland next to a garden in lyre bird disturbed litter under *Eucalyptus maidenii* and *E. globoidea* plus remnant rainforest and ferns beside creek. The soil is fine loam over clay on granite (Heather Meek, pers. comm., 22.vi.1999).

Genus *Digaster* Perrier

Digaster Perrier, 1872: 94–96; Beddard, 1895: 484; Michaelsen, 1900: 196, 1907: 162; Stephenson, 1930: 839; Jamieson, 1975: 267–269, Blakemore, 1997b: 1815–1816.

Diagnosis. Setae lumbricine. Male pores and pores of racemose prostates combined on 18 (or its homeotic equivalent). Penial setae absent or present. Two gizzards (sometimes three) in some (or all) of 5–7; extramural calciferous glands absent; typhlosole absent or present. Spermathecae two pairs with one or more discrete or sessile diverticula. Meronephric, avesiculate.

Some species have suppression of the first segment (*D. anomala* Jamieson, 1970, *D. lumbricoides* and the newly described *D. eastoni*) thus reducing these segmental counts by one.

Type species. *Digaster lumbricoides* Perrier, 1872, from Port Macquarie, NSW. (Types in the Muséum national d'Histoire naturelle, Paris).

Included species. Approximately 23 species are presently known as are variously listed in the references given in the generic synonymies above.

Distribution. Central coastal NSW to southeastern Qld.

Remarks. The most recent treatments of this genus are by Blakemore, (1994a, 1997b).

Digaster eastoni n.sp.

Fig. 19

Material examined. HOLOTYPE: AM W24503 (H), Mt Warning, northeastern NSW, c. 28°23'S 153°17'E, Ed Easton, 21.iii.1983, "Jar 31 Sp 21", (mature, posterior amputee, figured and dissected). PARATYPES: all same details as H, ANIC RB.98.2.46, (P1), (aclitellate juvenile, dissected); AM W24504, (P2–P4), (three specimens, one juvenile, and two immatures that agree superficially, plus three tail fragments).

External features (note: anterior segment suppressed, so all counts in following description should be increased by one to give normal segmentation). Body stout, first segment suppressed (but setae retained in P1). Lengths, mm: 70+ (H), 70–75 (P1–P2). Width: c. 3.5 mm. Segments: 280 (P1). Colour: unpigmented in alcohol; clitellum brick red. Prostomium: short pro-epilobous. Clitellum: ½12–½18. Dorsal pores: open from 4/5 (minute in 3/4 in P1), occluded on clitellum. Setae: 8 per segment, in regular series. Nephropores: small pores seen only on clitellum at anterior of segments equatorially. Spermathecal pores: two pairs in 6/7/8 in setal *a* lines. Female pore: single mid-ventral on 13. Male pores: on small mounds in *ab* lines on 17 conjoined within tumid pad that extends beyond *b* lines and encompassed marking in 16/17. Genital markings: large flat pad in position of 16/17 but distending and obscuring this furrow ventrally (H, P1, P2).

Internal anatomy. Septa: 6/7–10/11 increasingly thick. Gizzards: muscular in 5 and 6. Oesophagus: not especially dilated but thick walled with internal rugae in ½12–½17. Nephridia: avesiculate meroic, scattered tubules on body wall, reducing in number after clitellum to give about 10 per side; not tufted in anterior. Vascularization: dorsal blood vessel single; hearts 9–11 from weak supra-oesophageal vessel. Spermathecae: two pairs in 6 and 7, spherical ampulla on short duct with medium-sized clavate diverticulum ectally. Male organs: holandric, iridescent testes and funnels in 9 and 10; seminal vesicles paired, racemose flat posteriorly in 8 and elongate anteriorly in 11. Ovaries: extensive egg-strings and oviducts in 12; no ovisacs found in 13. Prostates: bi-lobed racemose glands in 17; penial setae absent but many tendons surround duct. Intestine: origin in ½17; typhlosole absent; contains grey soil with quartz and obsidian grits.

Remarks. *Digaster eastoni*, like *Digaster lumbricoides*, has suppression of the anterior segment; however, in *D. lumbricoides* the prostates are not bilobed and the seminal vesicles are in 10 and 11, rather than 8 and 11 as here. Other distinctive features of *Digaster eastoni* are the single female pore on 13, the large genital pad in 16/17, and the bilobed prostates.

Etymology. Named after the collector.

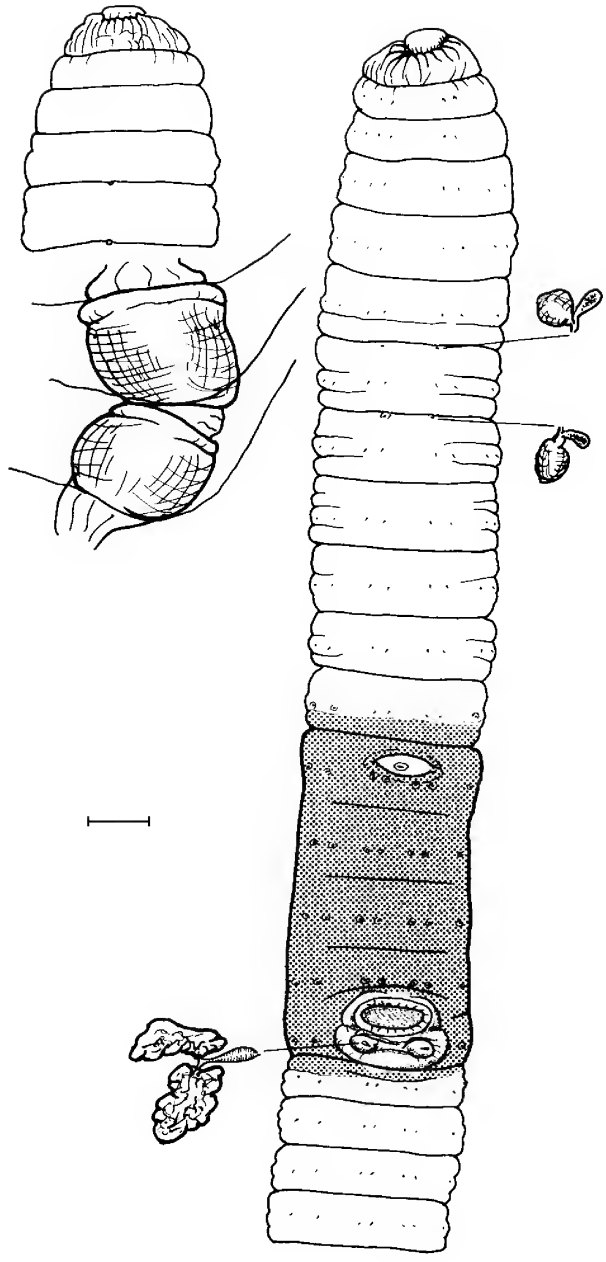

Figure 19. *Digaster eastoni* n.sp., ventral view of holotype with dorsal view of prostomium (first segment suppressed); gizzards in segments 5 and 6; spermathecae; and bilobed lhs prostate in 17. Scale 1 mm.

Distribution and habitat. In addition to *Digaster eastoni*, species from Mt Warning identified during the current study include *Heteroporodrilus editus*; *Fletcherodrilus fasciatus* (Fletcher, 1890) (specimen AM W24494 ex "Jar 31, Sp 22 Ed Easton 21 March 1983"); *Digaster lamingtonensis* Michaelsen, 1916 (specimens AM W24496 ex "Jar 31, Sp 19 1100 ft 21 March 1983" and AM W24463 "Jar 33 sp 5 Ed Easton 26 March 1983"); *Anisochaeta monsmonitionis* (Blakemore, 2000) and various other undescribed *Anisochaeta* spp. (AM W21717 ex "Jar 31 Sp 31"; W24501 and W24502 ex "Jar 30, Sp 31 21 March 1983, Lyrebird Lookout").

Discussion

The number of new species described in this paper, and the continuing need to resolve ambiguities for several known species, are indicative of the current state of knowledge of the fauna, supporting the conclusion by Abbott (1994: 117) that "Australia's indigenous species of earthworms are poorly known". Reasons for this deficit are not immediately obvious as earthworms are:

1 ubiquitous in soils capable of supporting plants;
2 they are vitally important, both ecologically and economically, for their role in recycling organic matter and in maintaining fertile soils;
3 native species are perfectly adapted to Australian soils and climates,
4 their process of identification is less complicated than for some other soil invertebrates (e.g., microscopic nematodes, collembolans or mites);
5 they have popular appeal; and,
6 from as early as 1861 they were initially subject to enthusiastic study.

Perhaps one reason that sustained research is frustrated, again taken from Abbott (1984), is due to "uncertainties about synonymy and higher level taxonomy, particularly at the generic level". Several conflicting taxonomic schemes are currently in use and confusion will persist unless these are resolved. Until such a time, perhaps the most pragmatic and convenient solution is to revert to the systems devised by Michaelsen (1900, 1907), which, despite some detraction, are for the most part still phylogenetically valid and form the basis of most subsequent schemes (Lee, 1994).

Few natives have been studied in any detail, the only notable exception being *Megascolides australis*, the Gippsland Giant Earthworm (Spencer, 1888; Smith & Peterson, 1982; VanPraagh, 1995). Our knowledge of the distribution, diversity and biology of native earthworms in general is severely limited, and ecological studies are especially scarce (cf. Wood, 1974; Abbott *et al.*, 1985). It is hoped that the formal description of species as here will facilitate and encourage the overdue ecological study of native species in both natural and managed environments.

Species of *Heteroporodrilus* appear especially promising candidates for agro-ecological study (see Blakemore, 1994b; 1997c; Friend & Chan, 1995) as they are widely dispersed on the eastern seaboard and in fertile clay soil floodplains and catchments of the Murray-Darling basin through to the mallee region of Victoria and South Australia. For *Heteroporodrilus mediterreus*, Fletcher (1887b: 602) remarked that "No species has hitherto been recorded from so far inland as this; and its occurrence is of interest as showing that the dry interior, at any rate in proximity to rivers, is not destitute of earthworms, though remote from them, as far as I can learn at present, worms seem to be very scarce or are entirely wanting". Abbott (1994) plotted the known distributions of native species, supporting Fletcher's observation, but stressed the importance of moisture retaining refugia for harbouring earthworms. Knowledge of the distribution of *Heteroporodrilus* in the southeastern states has now been extended, the genus has

Figure 20. Known distribution of *Heteroporodrilus* and *Plutellus* species in relation to the Murray-Darling Basin. (Background map courtesy of the Murray-Darling Basin Commission). Abbreviations: H.bi—*Heteroporodrilus bitenax*; H.bo—*H. bongeen*; H.ca—*H. canaliculatus*; H.di—*H. dioecius*; H.do—*H. doubei* (note: *H. clarkei* and *H. minyoni* occur nearby); H.ed—*H. editus*; H.hi—*H. hirthi*; H.ka—*H. kaputar*; H.me—*H. mediterreus*; H.nam—*H. namoi*; H.nar—*H. narrabri*; H.ox—*H. oxleyensis*; H.sh—*H. shephardi*; H.sl—*H. sloanei*; P.bar—*Plutellus barringtoni*; H.tr—*H. tryoni*; P.buc—*Plutellus buckerfieldi*; P.het—*P. heteroporus*; P.man—*P. manifestus*. (Details of distribution of Queensland species are given in Blakemore, 1994b).

previously been found to be particularly diverse in southern Queensland where three or four species can often be obtained in the same sample from certain sites (Blakemore, 1994b).

Considering biodiversity "hotspots", the current study appears to show that the Mt Warning locality, with more than six natives, has most variety. However, meaningful conclusions on regional biodiversity remain elusive given the present patchiness of survey—perceived diversity still relates largely to collection effort (which has tended to centre around populous areas), and to taxonomic treatment rather than to the actual situation. This deficit is graphically illustrated in the huge unsampled voids that isolate the known distribution points of *Heteroporodrilus* in the massive Murray-Darling basin (Fig. 20). For this reason the keys to species given above can only be considered provisional: numerous additional species undoubtedly await

discovery and description. A remedy to this would require more strategic survey from unrepresented regions and habitats at those times when earthworms are most active, as indeed had been assiduously undertaken by Ed Easton in 1983. The delay in formal description of this collection exemplifies the need for concurrent taxonomic work.

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Carboniferous and Permian Leaioidea (Branchiopoda: Conchostraca) from Australia: Taxonomic Revision and Biostratigraphic Implications

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ABSTRACT. A taxonomic revision of Australian leaioid faunas has reduced, by synonymy, the known Early Carboniferous taxa to three species viz., *Hemicycloleaia andersonae* (Tasch, 1979), *H. grantrangicus* (Tasch, 1979) and *Rostroleaia carboniferae* (Tasch, 1979); and the known Late Permian taxa to three species viz., *Hemicycloleaia mitchelli* (Etheridge, 1892), *H. discoidea* (Mitchell, 1925), and *H. deflectomarginis* (Tasch, 1979). The revision establishes a consistent taxonomic nomenclature to facilitate comparisons with extra-Australian leaiid species, and their correlations. Particular attention is paid to the correlation of the Late Permian leaioid and estheriid faunas of the Newcastle Coal Measures (NCM) of the Sydney Basin, with those of the Lebedevian of the Lower Tungus and Nordvik Basins, northern Siberia, which in turn, indicate a correlation (Lozovsky, 1998) with the Late Tatarian Vjatian (Luptug member) horizon of the Russian Platform. We speculate that the conchostracans may have lived in estuaries and ephemeral relict water bodies along a coastal plain, and that their eggs were dispersed either by wind, by minor marine incursions, or by both of these processes. Such marginal marine influences could partly explain the widespread distribution of Mitchell's Late Permian (Tatarian) conchostracan species.

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The Conchostraca are small branchiopod crustaceans with a weakly mineralised bilaterally compressed shell, in which the valves are joined by a ligament in a simple elevated fold. Post-Palaeozoic species appear to have lived in a lacustrine milieu, as do extant species; but some Palaeozoic species may have been adapted to brackish paralic environments (Webb, 1979; Chen & Shen, 1985). Like the Ostracoda, they are potentially useful biostratigraphic and palaeoecologic indicators. The Leaioidea are easily distinguished from other superfamilies of Conchostraca on the basis of valves bearing up to five radial carinae, which first appear in the ontogeny on the umbo, and in later growth

stages extend towards the free margin. Leaioids first appear in the geological record, together with representatives of other superfamilies (Estheriteoidea, Eosestherioidea, and Lioestherioidea), in the Devonian. Unlike these taxa, which are well represented in the Mesozoic, with some families still extant, the leaioids appear to have become extinct by the end of the Palaeozoic.

Published research on Australian leaioid conchostracans has so far been concentrated on faunas from the Lower Carboniferous, and the Upper Permian. Early Carboniferous leaioid taxa were described from the subsurface Anderson Formation, in the Canning Basin, Western Australia (Tasch & Jones, 1979); and from the Raymond Formation in the Drummond Basin, Queensland (Tasch, 1979). Late Permian leaiids were described from the Newcastle Coal Measures (NCM) in the Sydney Basin (Etheridge, 1892; Mitchell, 1925); these were the first leaiids to be reported from Australia, at a time when very little was known about Palaeozoic conchostracans. This pioneering work has been a major source reference for later taxonomic studies of leaiids in other parts of the world, several of which have misinterpreted Mitchell's (1925) type material, as discussed below. Tasch (1987) addressed these problems in a revision of Mitchell's material, which itself resulted in further problems. Other Late Permian leaiid taxa conchostracans have been described from the Blackwater Group in the Bowen Basin, Queensland (Tasch, 1979).

The aim of the present paper is to prepare a consistent taxonomy of the leaioid taxa from Australia to provide a comparison with those from overseas, and to evaluate their age significance. Particular attention has been paid to the correlation of the leaioid and estheriid faunas of the Upper Permian NCM. All type and figured specimens referred to in this paper are deposited in the Commonwealth Palaeontological Collection (under the prefix CPC) of the Australian Geological Survey Organisation (AGSO), formerly Bureau of Mineral Resources (BMR), Canberra; in the Palaeontological Collection of the Australian Museum, Sydney (under the prefix F); and in the Palaeontological Collection of the Department of Earth Sciences, University of Queensland, Brisbane (under the prefix UQF).

Previous studies of Australian Leaioid Conchostracan faunas

Sydney Basin. Leaiids were first found in Australia by John Mitchell in 1890, in loose chert that was used for road building at Charlestown, near Newcastle, New South Wales. The specimens were described by Etheridge (1892) under the name *Leaia mitchelli*, thirty years after Jones (1862) described the genus *Leaia* from the late Mississippian of North America. Mitchell (1925) described an additional 13 species referred to this genus and two unnamed species which he regarded as indeterminate, from material that he later collected *in situ* from localities within the Upper Permian NCM near Belmont and at Merewether Beach (Fig. 1).

Five of Mitchell's leaiid species were selected by overseas authorities (Kobayashi, 1954, and Novozhilov, 1952, 1954, 1956, 1958) as type species for new genera based, not on a first-hand examination of his material, but solely on his photographic figures, many of which had been retouched with black and white ink (Table 1). An additional five "new species" based on Mitchell's (1925) material, were introduced by Novozhilov (1956) [*Australoleaia miklouchomaklayi, Brachiorrhynchia chertensis*, and *Cycloleaia cyclica*], and by Kobayashi (1954) [*Trileaia sulcata* and *T. etheridgei*].

Subsequently, both Tasch (1969, 1979), and Chen & Shen (1985) considered that most of these genera are synonyms of *Leaia* Jones, 1862 or *Hemicycloleaia* Raymond, 1946. Tasch (1987) restudied and published new photographs of Mitchell's type specimens. By synonymy, he reduced the number of species introduced by Mitchell and Kobayashi from 16 to 12; the three species introduced by Novozhilov (1956) were not discussed. Tasch (1987) proposed one new species, *Leaia (Leaia) oblongoidea*, based on an incomplete carapace amongst Mitchell's illustrated specimens, and collected additional material from the NCM, from which he described a further three leaiid species [*L. (Hemicycloleaia) immitchelli, L. (H.) kahibahensis* and *L. (H.) magnumelliptica*]. Excluding the three above-mentioned "new species" introduced by Novozhilov (1956), which we regard as invalid (see below), the total number of leaiid species described from the NCM, after Tasch's (1987) analysis, stands at sixteen.

Bowen Basin. Leaiids were first recognised in the Bowen Basin by Dickins (in Veevers *et al.*, 1964: 85) from the Upper Permian Blackwater Group, on the eastern flank of the northern part of the basin. A single sample consisting of three specimens was collected by M.A. Randal in 1960 from a locality (CL 314/6), about 79.5 km northeast of Clermont (Clermont 1:250 000 sheet; Fig. 2). Tasch (1979) described this limited material as a new species *Leaia (Hemicycloleaia) deflectomarginis* and "*Leaia (Hemicycloleaia)* sp. undet. 1".

Canning Basin. Carboniferous conchostracans were first recognised in Western Australia by Öpik (in McWhae *et al.*, 1958), who identified leaiids in core samples taken from the Anderson Formation, penetrated by WAPET Grant Range No. 1 Well. This well (18°00'48"S 124°00'22"E) was

Table 1. List of Mitchell's (1925) leaioid species selected as type species for invalid genera introduced by Novozhilov (1952, 1954) and Kobayashi (1954).

Leaia quadriradiata	= *Brachioleaia* Novozhilov, 1952; *Quadrileaia* Kobayashi, 1954
Leaia discoidea	= *Cycloleaia* Novozhilov, 1952; *Discoleaia* Kobayashi, 1954
Leaia collinsi	= *Australoleaia* Novozhilov, 1954
Leaia quadrata	= *Gonioleaia* Novozhilov, 1952
Leaia belmontensis	= *Trileaia* Kobayashi, 1954

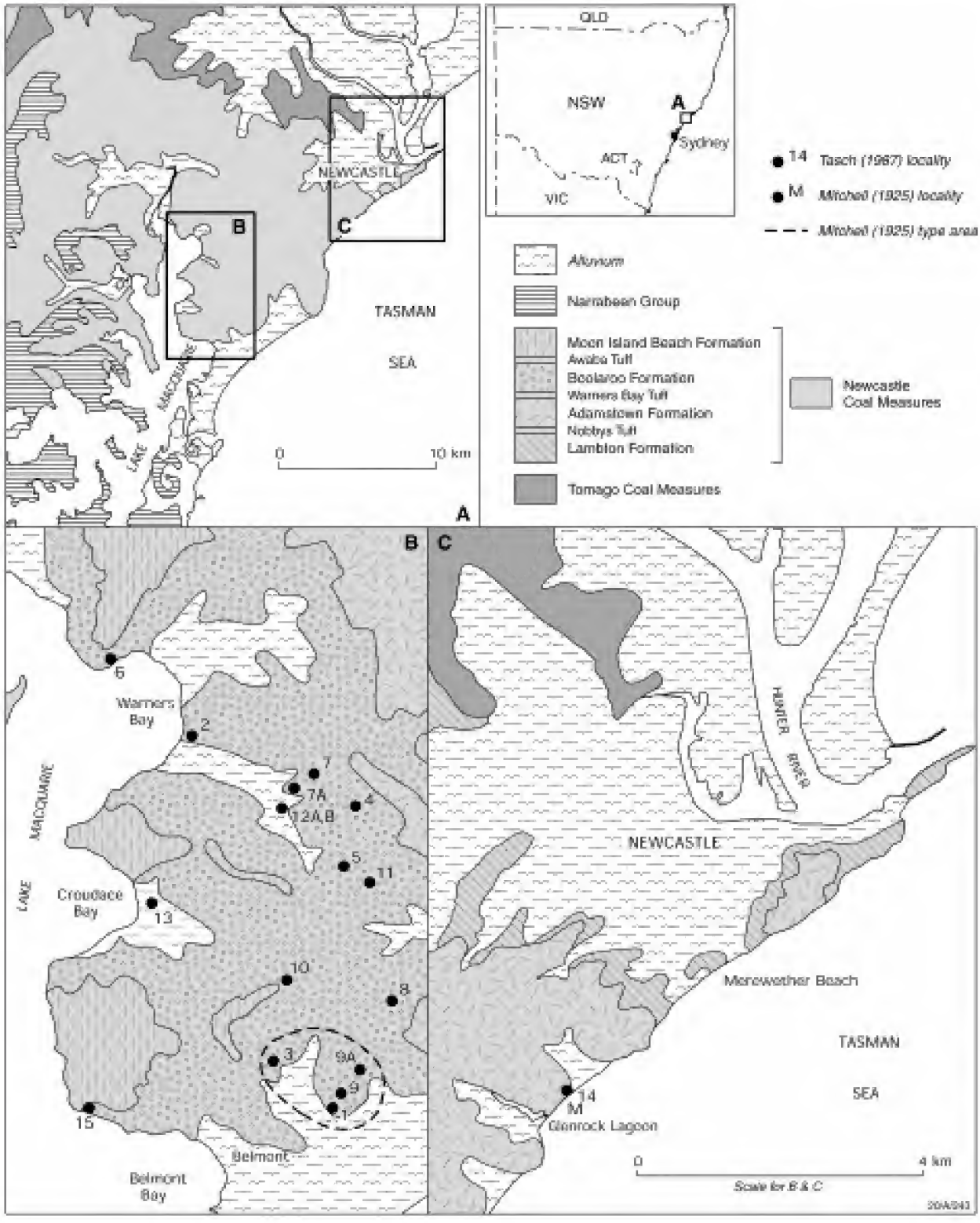

Figure 1. Locality maps Newcastle area, Sydney Basin. A—distribution of the Newcastle Coal Measures; B—distribution of conchostracan localities (Mitchell, 1925; Tasch, 1987) within the Boolaroo Formation in the Lake Macquarie area; C—distribution of conchostracan localities within the Lambton Formation (Mitchell, 1925, 1927; Tasch locality 14).

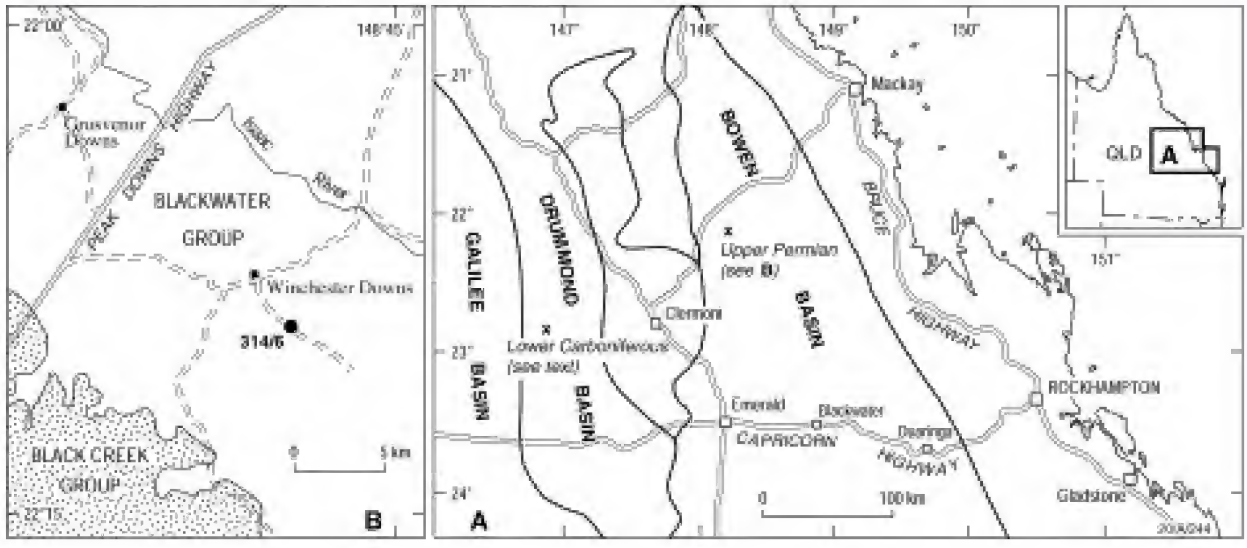

Figure 2. Locality maps of the Clermont area, Queensland, showing distribution of conchostracans in the Upper Permian Blackwater Group, Bowen Basin, and the Lower Carboniferous Raymond Formation, Drummond Basin.

drilled about 90 km south-southeast of Derby (Mount Anderson 1:250 000 sheet area) on the axis of the Grant Range Anticline within the Fitzroy Trough of the northern Canning Basin (Fig. 3). The sequence between 7900 feet (2408 m) and 12915 feet (3936 m; total depth) in Grant Range No. 1, designated by McWhae *et al.* (1958) as the type section of the Anderson Formation, consists of interbedded sandstone, siltstone and shale, with minor limestone, dolomite and anhydrite. Öpik determined the genus *Hemicycloleaia* in the leaiid sequence between 7907 and 8536 feet, which he regarded as Late Carboniferous (Westphalian-early Stephanian) in age. Bischoff (1968) concluded that this part of the sequence was deposited in a brackish estuarine or deltaic environment. The leaiid fauna was examined by Tasch (in Tasch & Jones, 1979), who described seven species belonging to four genera: *Monoleaia* Tasch, 1956, *Leaia* Jones, 1862, *Rostroleaia* Novozhilov, 1952, and *Limnadiopsileaia* Tasch, 1962. He also described two indeterminate species belonging to *Cyzicus*, and a species doubtfully referred to the Cretaceous genus *Ellipsograpta* Zhang, 1957.

Drummond Basin. Leaiid conchostracans were first recorded from Queensland by Hill (1957), who reported on collections made by Shell (Queensland) Development Pty Ltd geologists from two levels in the Lower Carboniferous sequence of the Drummond Basin (Olgers, 1972) viz., the top of the Telemon Formation, and the stratigraphically younger Ducabrook Formation. As a result of oil exploration by FRANCAREP, de Bretizel (1966) recorded a leaiid species from a third level, lying stratigraphically between these formations, from the Raymond Formation. This formation consists of quartzose sandstone and green mudstone, and attains a maximum thickness of 750 m in the southern part of the Drummond Basin (Playford & Jell, 1985). The leaiid specimens were collected by P. de Bretizel in 1963 from sites in the Narrien Range, 80 km W of Clermont (Galilee 1:250 000 sheet; Fig. 2). Although the precise localities are not known, they were collected from the top of section 70, and the base of section 75 (of de Bretizel, 1966: 83–84). The associated fauna included abundant fish (crossopterygian and palaeoniscoid) remains, malacostracan arthropods, and the polychaete annelid *Spirorbis* (Turner, 1993). In the absence of diagnostic marine fossils, this fauna is indicative of a brackish estuarine or deltaic environment (de Bretizel, 1966). For the same reason, a precise age for the Raymond Formation is difficult to determine; it may be within a ?late Tournaisian to early Viséan range. Turner (1993) suggested an early–mid Viséan age for the microvertebrate assemblage, which she described from the Raymond Formation. The leaiid species from the Raymond Formation, figured by Hill & Woods (1964) as *Leaia (Dolicholeaia?)* sp., was later described by Tasch (1979) as *Leaia (Hemicycloleaia) drummondensis*.

Localities and stratigraphic position of Late Permian conchostracan faunas

Bowen Basin. The leaioid species *Hemicycloleaia deflectomarginis* (Tasch, 1979) came from a single locality (CL 314/6) shown on the Clermont 1:250 000 sheet area (Olgers, 1969) at grid reference E 648767 N 2232877. M.A. Randal collected the specimens in 1960 from the Upper Permian Blackwater Group from a site 4.2 km SSE of Winchester Downs Homestead. This site is 2.0 km west of the westernmost limit of the CRA Limited Winchester South Coal Deposit (EPC486; Wilton, 1995). The stratigraphic position of the site is within the topmost Fort Cooper Coal Measures either within or just below the Yarrabee Tuff Bed; this tuff is overlain by the Rangal Coal Measures, the uppermost unit of the Blackwater Group (Fig. 9).

Sydney Basin. Mitchell's (1925) leaioid species came mainly from two areas within the NCM, the chert (tuff) quarries near Belmont (Fig. 1B), and the foreshore at Merewether Beach (Fig. 1C). Tasch's (1987) revision used

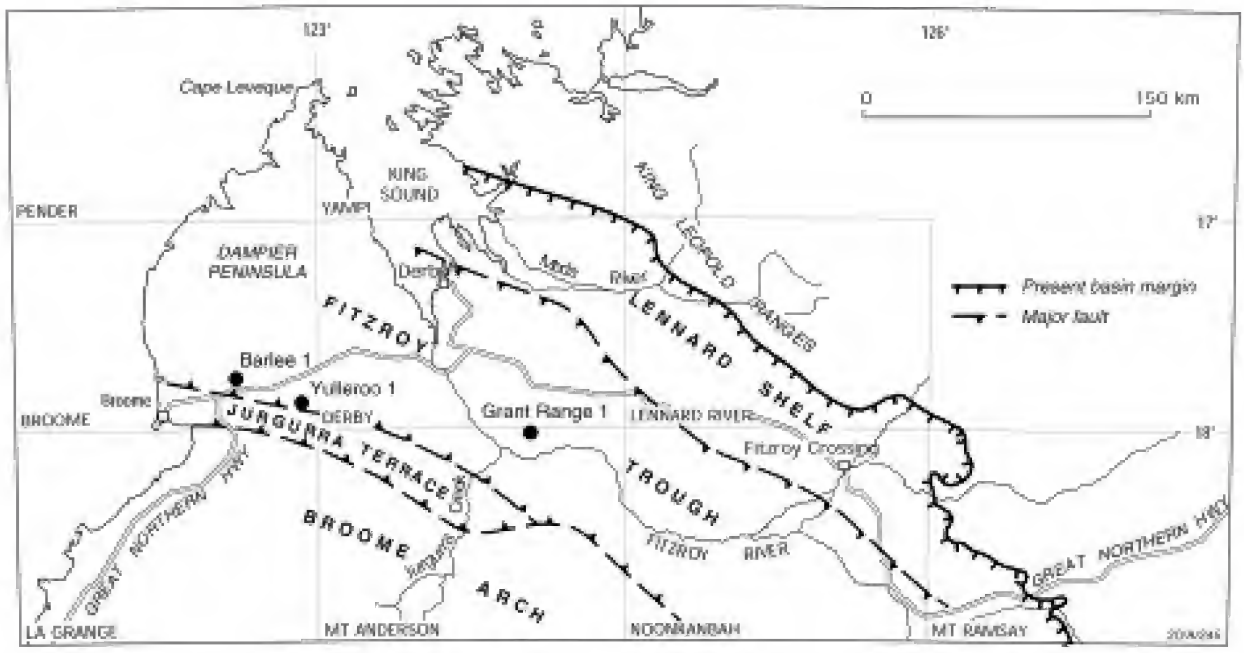

Figure 3. Locality map of the Fitzroy Trough, Canning Basin, showing the sites of those wells that contain Lower Carboniferous fossils within the subsurface Anderson Formation, which are discussed in the text.

the stratigraphic nomenclature and subdivision of the NCM after McKenzie & Britten (1969) and modified by the NSW Standing Committee on Coalfield Geology of NSW (1975). In this paper, the conchostracan localities of Mitchell (1925, 1927), and of Tasch (1987) are referred to the revised NCM stratigraphy as ratified by the NSW Standing Committee on Coalfield Geology in June 1992 (appendix 2 in Hawley & Brunton, 1995: 69–84), as modified by Little *et al.* (1996) (Fig. 4).

The Belmont localities contain two leaioid species (as revised here), *Hemicycloleaia discoidea* (Mitchell, 1925) and *H. mitchelli* (Etheridge, 1892), and three unribbed conchostracan species described by Mitchell (1927) as *Estheria belmontensis, E. glabra*, and *E. linguiformis*; [all three species referred by Raymond, 1946 to his genus *Pseudestheria*; and later referred by Tasch, 1987 to *Cyzicus (Euestheria); Palaeolimnadia (Palaeolimnadia)*; and *Palaeolimnadia? (Grandilimnadia?)* respectively]. The precise location of Mitchell's original Belmont site is equivocal. According to Knight (1970), Mitchell's original outcrop in the Belmont area was located 0.5 mile north of the John Darling Colliery, at a site 2.2 km NNE of Belmont. Its biota consists of leaioids associated with other conchostracans, and a *Glossopteris* flora came from a chert bed about 75 cm thick (the Belmont insect bed), that was later traced to other localities between Belmont and Warner's Bay on Lake Macquarie (Knight, 1970). Tasch, however, regarded a site on the northwestern shore of Belmont Bay (M15, Tasch, 1987, fig. 8), as Mitchell's original Belmont locality; this is based on a possible misinterpretation.

The only locality detail Mitchell provided for his Belmont leaioid and insect collections in the Newcastle Coal Measures was "chert quarries, near Belmont" (Mitchell, 1925: 441–443). He described the stratigraphic position of these localities as "a short distance above the old Cardiff Coal Seam [= Australasian Coal Seam (David, 1907: 251)] worked on the north-western shore of Belmont Bay (Great Northern Seam of David)" (Mitchell, 1925: 443). This statement matches the information Mitchell provided earlier to Tillyard (1917) on the stratigraphic position of the Belmont insect beds, but is in conflict with his correction, in the same paper (Mitchell, 1925: 439–440). The coal seam closest to, and above, the Belmont leaioid and insect fauna was misidentified by Mitchell as the Cardiff Seam. It is clear that this seam is the one bracketed by the Great Northern Coal above, and the Upper Pilot Coal below, which David (1907: 255) termed the Fassifern Seam.

Tasch (1987) correctly interpreted Mitchell's "old Cardiff Coal Seam" as the Fassifern Seam, and because Mitchell specified that the leaioids were above that coal seam, he inferred that Mitchell's original locality is within the Awaba Tuff. He then assumed that Mitchell's original site was on the northwestern shore of Belmont Bay (M15 in Tasch, 1987, fig. 8), but Tasch did not record conchostracans, or collect samples, from this site. However, we regard Mitchell's statement (quoted above) as simply implying a stratigraphic position, and not a precise geographic locality for the old Belmont chert (tuff) quarries. Mitchell's conchostracan specimens, which were associated with abundant insect remains, could have come from one or several of the localities visited and collected by Tasch (1987) e.g., his stations 3 (still named Belmont quarry), 1 (entrance to John Darling Colliery) and 9A,9B (just north of John Darling Colliery). Indeed, Knight (1970: 251) thought that Mitchell's original outcrop was located 0.5 mile north of the John Darling Colliery, at a site 2.2 km NNE of Belmont. Its biota, consisting of leaioids associated with other conchostracans and a *Glossopteris* flora, came from a chert (tuff) bed about 75 cm thick (the Belmont insect bed), that

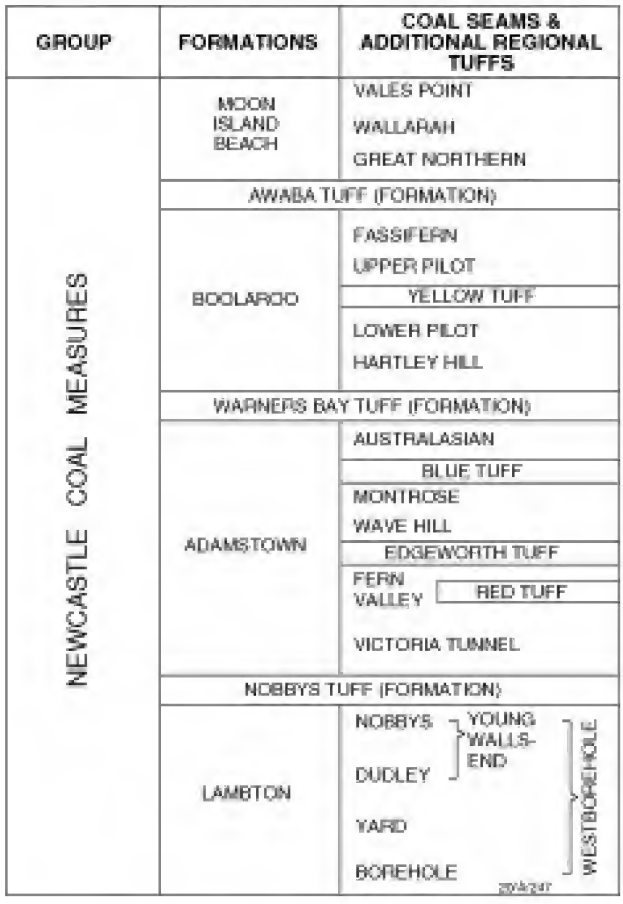

Figure 4. Current stratigraphic nomenclature of the Newcastle Coal Measures (after Hawley & Brunton, 1995, and Little *et al*., 1996, fig. 2).

was later traced to other localities between Belmont and Warner's Bay on Lake Macquarie (Knight, 1970). No ostracods have ever been found in association with the conchostracan samples.

According to Knight (1970) the Belmont insect bed is below the Fassifern Coal Seam, which suggests the same stratigraphic position for the leaioids in the Belmont chert (tuff) quarries. From Tasch's (1987: 19) study, the conchostracans in the Belmont area are distributed between the Upper Pilot Seam and the Fassifern Seam. Of all the localities from which he collected in the Belmont area, only two (Tasch stations 6 and 10) were above the Fassifern Seam. In terms of the revised NCM stratigraphy (appendix 2 in Hawley & Brunton, 1995), all the Belmont conchostracan localities of Mitchell (1925, 1927) and of Tasch (1987) were collected from the upper part of the Boolaroo Formation (Fig. 9).

The Merewether Beach locality (0.8 km NNE of Glenrock Lagoon; Fig. 1C) contains *Hemicycloleaia discoidea* (Mitchell, 1925), originally described as *Leaia compta*, from the Dirty Coal Seam (Mitchell, 1925: 445), which is now known as the Dudley Coal Seam. The label on the rock fragment containing the type specimen (F 25424) inscribed "From just above Dirty Seam", confirms Tasch's (1987: 23) comment that this species occurred above the Dudley seam. We presume this locality is the same one (i.e., "a short distance SW of the outflow of the Newcastle sewage") from which Mitchell (1927) described five unribbed conchostracans: *Estheria lenticularis* (type species of *Cyclestherioides* Raymond, 1946), *Estheria novocastrensis, E. lata, E. trigonellaris*, and *E. obliqua* [referred by Raymond, 1946 to his genus *Pseudestheria*; and by Tasch, 1987 to *Cyzicus (Euestheria)*], from "a few feet below the Dirty Seam …". In terms of the revised NCM stratigraphy (appendix 2 in Hawley & Brunton, 1995), the Merewether Beach locality of Mitchell (1925, 1927) is in the upper part of the Lambton Formation. Tasch (1987: 259) subsequently collected from this locality (his station 14), a leaiid specimen (subsequently lost), *Cyzicus (Euestheria) novocastrensis*, and *C. (Euestheria) lata.*

Taxonomic revision of Australian Leaioidea

The taxonomy of fossil conchostracans is mainly based on the characteristics of the thin carapace and minute ornamentation of growth bands, because the soft bodies and appendages are seldom preserved in fossils (Chen & Hudson, 1991). For the superfamily Lioestherioidea, the morphological taxonomy is mostly dependent upon the features of the umbo (its size, whether it bears a node or spine) or dorsal margin (recurved growth lines near the dorsal margin); for the Eosestherioidea, it is based entirely on the variety of minute ornamentation of growth bands; and for the Leaioidea, the taxonomy is based on the numbers of radial carinae present, and partly on the recurved growth lines near the dorsal margin. In most fossil conchostracans, carapace outline varies only from elliptical, oval, or subquadrate to subcircular or semicircular, with umbones generally placed between the middle point and the anterior end of the dorsal margin; therefore differences in carapace outline are not regarded as superfamilial characters, but rather as characters (together with the number of growth lines) which serve to distinguish between species.

Within the Leaioidea, differences in angular measurements between radial carinae (Fig. 5) have been used by some authors (e.g., Tasch, Novozhilov) to distinguish taxa at the species level, but in our opinion, these may be due to variation within a single species. Furthermore, fossil conchostracans are susceptible to deformation and are often found in a crumpled state, and the deformational variation of *Hemicycloleaia tricarinata*, as described by Feys (1953) is particularly salutary in this regard. Thus, discrimination of species and genera on form alone becomes difficult and tends to result in long lists of subfamilies, genera and species based on forms which may well be conspecific.

Early Carboniferous Leaioidea. Our revision of the taxonomy of Early Carboniferous leaiids from the subsurface Anderson Formation (late Viséan-earliest Namurian?) is based on a re-examination of Tasch's type specimens (Tasch & Jones, 1979), and has reduced by synonymy the original 9 species (referred to 5 genera) to 3 species (referred to 2 genera), viz., *Hemicycloleaia andersonae* (Tasch, 1979), *H. grantrangicus* (Tasch, 1979)

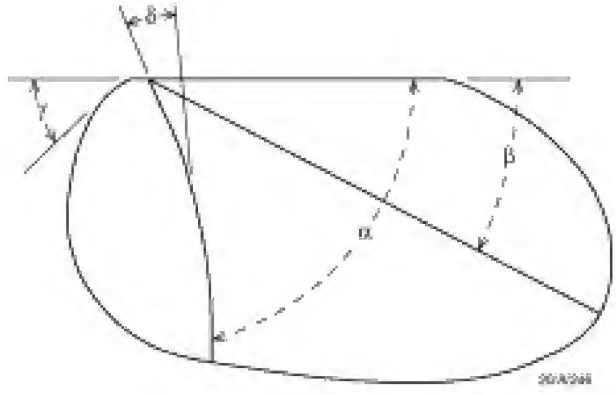

Figure 5. Leaioid conchostracan valve angles (after Tasch, in Tasch & Jones, 1979). Delta and gamma measure angular deviations from a straight line, represented respectively by the anterior rib (δ angle) and dorsal margin (γ angle). α and β angles are both measured from dorsal margin to the anterior rib (α angle) and posterior rib (β angle).

and *Rostroleaia carboniferae* (Tasch, 1979). Tasch & Jones (1979: 7) commented that the occurrence of *Monoleaia, Rostroleaia* and *Limnadiopsileaia* in the Anderson Formation represented the first records of these genera in pre-Permian rocks. Since then, Shen (1978, 1979) documented *Rostroleaia* in the Middle Devonian of South China, and in this paper we demonstrate that the specimens described as *Monoleaia australiata* Tasch, 1979 and *Limnadiopsileaia carboniferae* Tasch, 1979 belong to *Rostroleaia carboniferae* (Tasch, 1979). Also, we see no morphological reason to distinguish the Drummond Basin species, previously described as *Leaia (Hemicycloleaia) drummondensis* Tasch, from *Hemicycloleaia grantrangicus* from the Canning Basin (Table 2).

Late Permian Leaioidea. Our revision of the Late Permian leaiids from the NCM is based on a re-examination of Mitchell's (1925) type specimens, and a re-evaluation of Tasch's (1987) analysis of the same material. From our results, we consider that the taxonomies of Mitchell (1925) and other workers who have used his material (Kobayashi, 1954; Novozhilov, 1952, 1954, 1956, 1958; Tasch, 1987) represent examples of a tendency towards excessive splitting of fossil species (Table 3). An extreme example of this tendency, not only regards every specimen as a "new species", but also creates synonyms from Mitchell's syntypes, as exemplified by *Australoleaia miklouchomaklayi* Novozhilov, 1956 and *Cycloleaia cyclica* Novozhilov, 1956, which are objective junior synonyms of Mitchell's species *Leaia oblonga* and *L. discoidea*, respectively.

In our view, the number of species described by Mitchell (16, referred to the genus *Leaia*) should be reduced by synonymy to two, viz., *Hemicycloleaia mitchelli* (Etheridge, 1892) and *H. discoidea* (Mitchell, 1925). Furthermore, the four species described by Tasch (1987) from the NCM are junior synonyms of *H. mitchelli* (Etheridge, 1892). The limited material previously described from the Late Permian of the Bowen Basin as *Leaia (Hemicycloleaia) deflectomarginis* and *Leaia (Hemicycloleaia)* sp. indet. 1 (Tasch, 1979), belongs to a single species, *Hemicycloleaia deflectomarginis* (Tasch, 1979). Tasch (1979 p. 40, pl. 6, fig. 1) noted that the "slight downward flexure of the dorsal margin" in the latter species, is present in *Leaia pincombei* Mitchell, 1925 (a junior synonym of *Hemicycloleaia mitchelli* Etheridge, 1892; this paper). This feature, in both species, is probably due to crumpled preservation at the post-mortem stage.

Thus, three species of Late Permian leaioids are recognised in Australia viz., *Hemicycloleaia discoidea* (Mitchell, 1925), *H. mitchelli* (Etheridge, 1892) in the Sydney Basin, and *H. deflectomarginis* (Tasch, 1979) in the Bowen Basin. These species are larger, and have fewer growth bands, compared with those described from the Australian Carboniferous.

Table 2. Australian Leaiidae: Canning, Drummond and Bowen Basins.

Tasch, 1979 (in Tasch & Jones, 1979)	register number	revised name herein
Leaia (Leaia) andersonae	(CPC 17135)	= *Hemicycloleaia andersonae*
Leaia (Hemicycloleaia) rectangellipta	(CPC 17136)	= *Hemicycloleaia andersonae*
Monoleaia australiata	(CPC 17140)	= *Hemicycloleaia andersonae*
Leaia (Hemicycloleaia) grantrangicus	(CPC 17137)	= *Hemicycloleaia grantrangicus*
Leaia (Hemicycloleaia) tonsa	(CPC 17138)	= *Hemicycloleaia grantrangicus*
Leaia (Hemicycloleaia) longicosta	(CPC 17139)	= *Hemicycloleaia grantrangicus*
Leaia (Hemicycloleaia) drummondensis	(UQF 44310)	= *Hemicycloleaia grantrangicus*
Leaia (Hemicycloleaia) deflectomarginis	(CPC 17173A,B)	= *Hemicycloleaia deflectomarginis*
Leaia (Hemicycloleaia) sp. indet. 1	(CPC 17174)	= *Hemicycloleaia deflectomarginis*
Rostroleaia sp. (specimen destroyed)		= *Rostroleaia carboniferae*
	(CPC 33823; new)	= *Rostroleaia carboniferae*
Limnadiopsileaia carboniferae	(CPC 17141)	= *Rostroleaia carboniferae*

Table 3. Australian Leaiidae: Sydney Basin; list of species (Mitchell, 1925; Kobayashi, 1954; Tasch, 1987) regarded as junior synonyms of *Hemicycloleaia mitchelli* and *H. discoidea*.

***Hemicycloleaia mitchelli* (Etheridge, 1892)**	
Leaia mitchelli Etheridge, 1892	
Leaia mitchelli	(F 25426, F 25430, F 25487)
Leaia belmontensis Mitchell	(F 25429)
Leaia collinsi Mitchell	(F 25421)
Leaia elliptica Mitchell	(F 25463)
Leaia intermediata Mitchell	(F 25459)
Leaia oblonga Mitchell	(F 25420, F 25423)
Leaia ovata Mitchell	(F 25456)
Leaia paraleidyi Mitchell	(F 25454)
Leaia pincombei Mitchell	(F 25449)
Leaia quadrata Mitchell	(F 25468)
Leaia sp. indet., Mitchell	(F 25461) [= *Trileaia sulcata* Kobayashi, 1954]
Leaia sp. indet., Mitchell	(F 25427) [= *Trileaia etheridgei* Kobayashi, 1954]
Leaia (L.) oblongoidea Tasch	
Leaia (H.) immitchelli Tasch	
Leaia (H.) kahibahensis Tasch	
Leaia (H.) magnumelliptica Tasch	
***Hemicycloleaia discoidea* (Mitchell, 1925)**	
Leaia discoidea Mitchell	(F 25419; lectotype designed by Kobayashi, 1954)
	(F 25422; lectotype selected by Novozhilov, 1956)
Leaia compta Mitchell	(F 25421, in catalogue; F 25424)
Leaia latissima Mitchell	(F 25466)
Leaia quadriradiata Mitchell	(F 25465)

Systematic palaeontology

Order **Conchostraca** Sars, 1867

Suborder **Leaiina** Kobayashi, 1972

Superfamily **Leaioidea** Raymond, 1946

[*nom. transl.* Novozhilov, 1958; *ex* Leaiidae Raymond, 1946]

Remarks. The classification of the suborder Leaiina (*sensu* Kobayashi, 1972, 1973) adopted here differs from that proposed by Chen & Shen (1985), in that it is confined to the superfamily Leaioidea. This suborder originally included both the superfamilies Leaioidea Raymond, 1946 and Estheriellioidea Kobayashi, 1954.

The latter superfamily must now be excluded from the Conchostraca, and even from the Crustacea, because *Estheriella* Weiss 1875, the type-genus for both the family Estheriellidae and superfamily Estheriellioidea, must be referred to the Bivalvia. Investigations (by Chen Pei-ji) of the type specimens of the type species of *Estheriella* Weiss, 1875 [*E. costata* (Giebel 1857)], and of *Pseudestheriella* Novozhilov, 1956 [*Estheriella nodocostata* (Giebel, 1857); Jones, 1891], originally collected from the Lower Triassic Lower Bunter Sandstone of Germany, and now housed in the Natural History Museum, London (I 2533, I 2534 respectively), have confirmed Giebel's (1857) opinion that they have bivalve molluscan affinities.

At a lower supra-generic level, the subfamily Amphikoilinae Novozhilov, 1953, which was included by Chen & Shen (1985) in the family Leaiidae, must be also excluded from the Conchostraca, because Pogorevich (1975) has demonstrated that its type genus, *Amphikoilum* Novozhilov, 1953, is also a bivalve.

In this paper, we adopt the following modification of the earlier classification of Chen & Shen (1985) for the superfamily Leaioidea:

Monoleiolophidae—with one radial carina; includes *Monoleiolophus* Raymond, 1946, *Massagetes* Novozhilov, 1954, and *Petschoria* Zaspelova, 1962. [U. Carb.–U. Perm.]

Leaiidae—with two radial carinae and possibly a dorsal carina; includes *Leaia* Jones, 1862, *Hemicycloleaia* Raymond, 1946 and *Acantholeaia* Almeida, 1950. [M. Dev.–U. Perm.]

Praeleaiidae—with three to five radial carinae; includes *Praeleaia (Praeleaia)* Lutkevich, 1929, *P. (Hepuleaia)* Shen, 1978, *Paraleaia* Raymond, 1946 and *Eutrileaia* Shen, 1983. [M. Dev.]

Rostroleaiidae—with posterodorsally recurved growth bands along dorsal margin, and one to five radial carinae; includes *Rostroleaia* Novozhilov, 1952, *Limnadiopsileaia* Tasch, 1962 and *Pteroleaia* Copeland, 1962. [M. Dev.–U. Perm.]

Family **Leaiidae** Raymond, 1946

Diagnosis. Leaioidea with two radial carinae; a third carina may be present along the dorsal margin.

Genus ***Leaia*** Jones, 1862

1862 *Leaia* Jones, p. 116, pl. 5, figs. 11, 12.

Type species. *Cypricardia leidyi* Lea, 1855: 341 (by original designation); Upper Mississippian, Mauch Chunk Series (Chesterian), Pottsville, Pennsylvania, USA.

Diagnosis. Leaiidae with rectangular outline, bearing two radial carinae.

Range. Carboniferous.

Distribution. Europe?, North Africa and North America.

Remarks. It is difficult to separate transitional forms of *Leaia* and *Hemicycloleaia*, on the basis of carapace outline. In this paper, we prefer to confine the genus *Leaia* to those species with a rectangular carapace bearing two radial carinae, and without a dorsal carina.

Genus ***Hemicycloleaia*** Raymond, 1946

1946 *Hemicycloleaia* Raymond
1952 *Brachioleaia* Novozhilov
1952 *Cycloleaia* Novozhilov
1952 *Gonioleaia* Novozhilov
1952 *Dolicholeaia* Novozhilov
1952 *Kaltanleaia* Novozhilov
1952 *Lioleaia* Novozhilov
1953 *Leaia (Hemicycloleaia)* Raymond, Dechaseaux
1954 *Australoleaia* Novozhilov
1954 *Mimoleaia* Novozhilov
1954 *Siberioleaia* Novozhilov
1954 *Discoleaia* Kobayashi
1954 *Quadrileaia* Kobayashi
1954 *Trileaia* Kobayashi
1954 *Eoleaia* Kobayashi
1956 *Brachiorrhynchia* Novozhilov
1956 *Igorvarentsovia* Novozhilov
1965 *Cornoleaia* Molin
1969 *Leaia* Jones, Tasch
1978 *Kasacholeaia* Shen
1979 *Leaia (Hemicycloleaia)* Raymond, Tasch
1987 *Leaia (Hemicycloleaia)* Raymond, Tasch

Type species. *Hemicycloleaia laevis* Raymond, 1946: 286 (by origination designation); Upper Pennsylvanian, Conemaugh Series (Missourian) shale above lower Mahoning Sandstone, Conemaugh, Pennsylvania, USA.

Diagnosis. Leaiidae with elliptical, semicircular, subquadrate or ovate carapace, bearing two radial carinae; a third carina may be present along the dorsal margin.

Range. Middle Devonian to Upper Permian.

Distribution. Europe, Asia, Africa, North and South America, Australia and Antarctica.

Hemicycloleaia andersonae (Tasch, 1979)

Fig. 6a–d

1979 *Leaia (Leaia) andersonae* Tasch, p. 11, pl.1, fig. 1.
1979 *Leaia (Hemicycloleaia) rectangellipta* Tasch, p. 12, pl. 1, figs. 2–4.
1979 *Monoleaia australiata* Tasch, p. 13, pl. 2, fig. 4.
1987 *Leaia (Leaia) andersonae*; Tasch, p. 79.
1987 *Leaia (Hemicycloleaia) rectangellipta*; Tasch, p. 79.
1987 *Monoleaia australiata* Tasch, p. 79.

Diagnosis. Carapace small, elongate-elliptical or subelliptical anteriorly and subrectangular posteriorly in outline, 3.2–7.4 mm long and 1.9–4.4 mm high. Anterior carina somewhat arcuate and the posterior carina straight, dorsal margin thickened into third carina. α angle = 81–90°, β angle = 22–27.5°.

Remarks. With the exception of *Rostroleaia*, the eight species of Early Carboniferous leaioid conchostracans described by Tasch (in Tasch & Jones, 1979) from the Canning Basin, and the one species from the Drummond Basin, possess valves with two radial carinae, and a third carina, which is formed by a thickening of the dorsal margin. All species with these features may be referred to *Hemicycloleaia*. They can be subdivided into two groups based on the outline of the carapace: *H. andersonae* (Tasch) to include elliptical to subrectangular forms, and *H. grantrangicus* Tasch to include ovate to subsemicircular forms. An incomplete right valve described and figured by Tasch (in Tasch & Jones, 1979, pl. 2, fig. 4) as *Monoleaia australiata* possesses an anterior carina (Fig. 6b), which was concealed by incorrect lighting during photography.

Type locality and horizon. Grant Range No. 1 Well, core 62, 8530–8536 feet; Lower Carboniferous Anderson Formation. Also in core 52, 7907–7912 feet; same locality.

Hemicycloleaia grantrangicus (Tasch, 1979)

Fig. 6e–i

1964 *Leaia (Dolicholeaia?)* sp. Hill & Woods, p. c28, pl. cxiv, fig. 9.
1979 *Leaia (Hemicycloleaia) grantrangicus* Tasch, p. 12, pl. 1, figs. 5,6.
1979 *Leaia (Hemicycloleaia) tonsa* Tasch, p. 13, pl. 1, figs. 7,8.
1979 *Leaia (Hemicycloleaia) longicosta* Tasch, p. 13, pl. 2, figs. 1,2.
1979 *Leaia (Hemicycloleaia) drummondensis* Tasch, p. 39, fig. 5.
1987 *Leaia (Hemicycloleaia) grantrangicus*; Tasch, p. 79.
1987 *Leaia (Hemicycloleaia) tonsa*; Tasch, p. 79.
1987 *Leaia (Hemicycloleaia) longicosta*; Tasch, p. 79.
1987 *Leaia (Hemicycloleaia) drummondensis* Tasch, p. 79.

Diagnosis. Carapace broadly ovate or subsemicircular in outline, 4.3–7.8 mm long and 2.9–4.8 mm high. Short anterior carina gently arcuate and does not reach ventral margin; posterior carina generally long and bears weakly expressed nodes where growth lines cross it. α angle = 83–112.5°, β angle = 29–40°. Dorsal margin bears a carina reflected as a narrow flange.

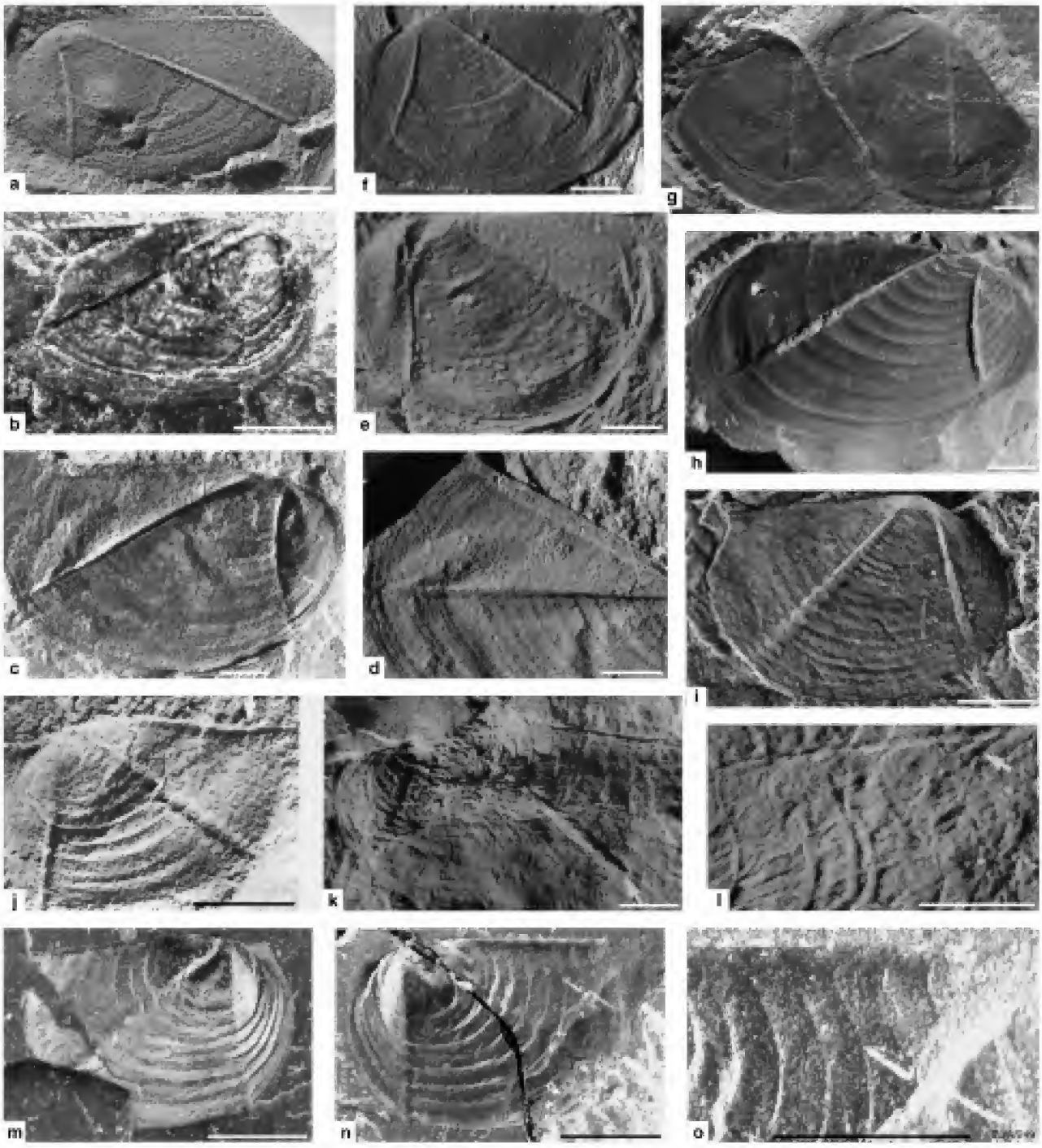

Figure 6. CARBONIFEROUS LEAIIDS, scale 1 mm. **a–d** *Hemicycloleaia andersonae* (Tasch): a—holotype, CPC 17135, left valve, WAPET Grant Range No. 1 Well, core 62 (8530–8536 feet), Anderson Formation; b—CPC 17140 (formerly *Monoleaia australiata* Tasch), right valve, WAPET Grant Range No. 1 Well, core 52 (7907–7912 feet), Anderson Formation; c,d—CPC 17136 (formerly *Leaia (H.) rectangellipta* Tasch), external mould of left valve, same locality as for b. **e–i** *Hemicycloleaia grantrangicus* (Tasch): e—CPC 17139 (formerly *Leaia (H.) longicosta* Tasch), external mould of right valve, same locality as for b; f,g—CPC 17138 (formerly *Leaia (H.) tonsa* Tasch), f, left valve, g, same left valve on right side and an internal mould of right valve on left side, WAPET Grant Range No. 1 Well, core 62 (8530–8536 feet), Anderson Formation; h—holotype, CPC 17137, right valve, WAPET Grant Range No. 1 Well, core 52 (7907–7912 feet), Anderson Formation; i—UQF 44310 (formerly *Leaia (H.) drummondensis* Tasch), right valve, Narrien Range, NW of Emerald, Drummond Basin, Raymond Formation. **j–o** *Rostroleaia carboniferae* (Tasch): j—specimen destroyed, (formerly *Rostroleaia* sp. Tasch), left valve, same locality as for h; k,l—holotype, CPC 17141 (formerly *Limnadiopsileaia carboniferae* Tasch), k, broken left valve (arrow points to the posterior radial carina) and partly external mould of another right valve with anterior radial carina, l, arrow points to the recurved posterodorsal margin, same locality as for h; m–o—CPC 33823 (new selected specimen from the original collection), m, external mould of left valve, same locality as for h, n, left valve, o, same specimen showing the recurved growth bands near the posterodorsal margin.

Remarks. We include *Leaia (Hemicycloleaia) tonsa* Tasch and *L. (H.) drummondensis* Tasch, as junior synonyms of *Hemicycloleaia grantrangicus*. Although the holotypes of *H. tonsa* and *H. drummondensis* possess more growth lines and have a slightly greater height/length ratio (0.67, 0.73), compared to the holotype of *H. grantrangicus* (0.62), we attribute these differences to ecophenotypic variation within a single species. As revised here, *Hemicycloleaia grantrangicus* differs from *H. andersonae* only in the configuration of the carapace. It has a height/length ratio ranging between 0.62 and 0.73, whereas in *H. andersonae* this ratio is less than 0.59. This difference could be due to dimorphism, because within other samples of leaiid populations, the valve of the female is frequently shorter than the otherwise similar male, which in turn, is generally narrower than the female. Thus *H. grantrangicus* and *H. andersonae* may be dimorphs of a single species.

Type locality and horizon. Grant Range No. 1 Well, cores 52, 7907–7912 feet; Lower Carboniferous Anderson Formation, Canning Basin, Western Australia. Also in core 62, 8530–8536 feet, same locality; and in Narrien Range, NW of Emerald, Lower Carboniferous Raymond Formation, Drummond Basin, Queensland.

Hemicycloleaia mitchelli (Etheridge, 1892)

Fig. 7a–n

1892 *Leaia mitchelli* Etheridge, p. 307.
1925 *Leaia mitchelli*; Mitchell, p. 440, pl. 41, figs. 1,2.
1925 *Leaia belmontensis* Mitchell, p. 445, pl. 42, fig. 15.
1925 *Leaia collinsi* Mitchell, p. 446, pl. 43, fig. 16.
1925 *Leaia elliptica* Mitchell, p. 443, pl. 42, fig. 10.
1925 *Leaia intermediata* Mitchell, p. 440–441, pl. 41, figs. 3–4.
1925 *Leaia oblonga* Mitchell, p. 441, pl. 41, fig. 5, pl. 43, fig. 18.
1925 *Leaia ovata* Mitchell, p. 443–444, pl. 42, fig. 12.
1925 *Leaia paraleidyi* Mitchell, p. 442–443, pl. 41, fig. 8.
1925 *Leaia pincombei* Mitchell, p. 443, pl. 42, fig. 9.
1925 *Leaia quadrata* Mitchell, p. 446, pl. 43, fig. 17.
1925 *Leaia* sp. indet., Mitchell, p. 446, pl. 43, fig. 20.
1925 *Leaia* sp. indet., Mitchell, p. 446, pl. 43, fig. 21.
1952 *Gonioleaia quadrata* (Mitchell); Novozhilov, p. 1371, fig. 2d (= drawing of Mitchell, 1925, pl. 43, fig. 17).
1954 *Trileaia mitchelli* (Etheridge) Kobayashi, p. 108, 144–145, 161.
1954 *Trileaia belmontensis* (Mitchell); Kobayashi, p. 144, text-fig. 30 l.
1954 *Trileaia etheridgei* Kobayashi; Kobayashi, p. 108, 144, 157.
1954 *Trileaia intermedia* [sic] (Mitchell) Kobayashi, p. 108, 145, 158.
1954 *Trileaia sulcata* Kobayashi; Kobayashi, p. 108, 144, 145.
1954 *Leaia collinsi* Mitchell; Kobayashi, p. 155.
1954 *Leaia elliptica* Mitchell; Kobayashi, p. 108, 166.
1954 *Leaia oblongata* [sic] Mitchell; Kobayashi, p. 109, 163.
1954 *Leaia ovata* Mitchell; Kobayashi, p. 163.
1954 *Leaia paraleidyi* Mitchell; Kobayashi, p. 163.
1954 *Leaia pincombei* Mitchell; Kobayashi, p. 164.
1954 *Australoleaia collinsi* (Mitchell); Novozhilov, p. 1241–1244.
1956 *Mimoleaia mitchelli* (Etheridge); Novozhilov, p. 63, pl. 11, fig. 3 (= Mitchell, 1925, pl. 41, fig. 2).
1956 *Australoleaia collinsi* (Mitchell); Novozhilov, p. 71, pl. 12, fig. 4 (= Mitchell, 1925, pl. 43, fig. 16).
1956 *Australoleaia miklouchomaklayi* Novozhilov; Novozhilov, p. 70, 71, pl. 12, fig. 3 (= *Leaia oblonga* Mitchell, 1925, pl. 43, fig. 18 only).
1956 *Hemicycloleaia belmontensis* (Mitchell); Novozhilov, p. 38, pl. 6, fig. 8 (= Mitchell, 1925, pl. 42, fig. 15).
1956 *Hemicycloleaia etheridgei* (Kobayashi); Novozhilov, p. 39, pl. 6, fig. 9 (= Mitchell, 1925, pl. 43, fig. 21).
1956 *Hemicycloleaia intermediata* (Mitchell); Novozhilov, p. 32, pl. 4, figs. 9,10. (Included *L. intermediata* pl. 41, fig. 3 and *L. elliptica* pl. 42, fig. 10).
1956 *Hemicycloleaia pincombei* (Mitchell); Novozhilov, p. 32, pl. 4, fig. 8 (= Mitchell, 1925, pl. 42, fig. 9).
1956 *Hemicycloleaia sulcata* (Kobayashi); Novozhilov, p. 39, pl. 6, fig. 10 (= Mitchell, 1925, pl. 43, fig. 20).
1956 *Leaianella paraleidyi* (Mitchell); Novozhilov, p. 58, pl. 10, fig. 2 (= Mitchell, 1925, pl. 41, fig. 8).
1956 *Mimoleaia ovata* (Mitchell); Novozhilov, p. 65, 66, pl. 11, fig. 8 (= Mitchell, 1925, pl. 42, fig. 12).
1956 *Siberioleaia oblonga* (Mitchell); Novozhilov, p. 26, 27, fig. 18, pl. 3, fig. 6 (= Mitchell, 1925, pl. 41, fig. 5 only).
1956 *Gonioleaia quadrata* (Mitchell); Novozhilov, p. 83, pl. 14, fig. 5 (= Mitchell, 1925, pl. 43, fig. 17).
1965 *Mimoleaia mitchelli*; (Etheridge); Novozhilov, pl. 6, figs. 1–3.
1965 *Leaianella paraleidyi*; (Mitchell); Novozhilov, pl. 7, figs. 5,6.
1987 *Leaia (Hemicycloleaia) mitchelli* Etheridge; Tasch, p. 82, 120–122, pl. 23, fig. 1, pl. 40, fig. 1, 2, pl. 41, fig. 1,4.
1987 *Leaia (Hemicycloleaia) collinsi* Mitchell; Tasch, p. 79, 122, pl. 22, fig. 3, pl. 40, fig. 3.
1987 *Leaia (Hemicycloleaia)* cf.*collinsi* Mitchell; Tasch, p. 80.
1987 *Leaia (Hemicycloleaia) elliptica* Mitchell; Tasch, p. 80, 125, pl. 23, fig. 4, pl. 41, fig. 7.
1987 *Leaia (Hemicycloleaia) etheridgei* (Kobayashi); Tasch, p. 126, pl. 41, fig. 6.
1987 *Leaia (Hemicycloleaia)* cf. *etheridgei* (Kobayashi); Tasch, p. 80, pl. 22, fig. 6.
1987 *Leaia (Leaia) oblonga* Mitchell; Tasch, p. 82,83, 123, pl. 23, fig. 6, pl. 40, fig. 7.
1987 *Leaia (Hemicycloleaia) ovata* Mitchell; Tasch, p. 83, 126, 127, pl. 24, fig. 2, pl. 41, fig. 8.
1987 *Leaia (Hemicycloleaia) paraleidyi* Mitchell; Tasch, p. 124, pl. 42, fig. 8.
1987 *Leaia (Hemicycloleaia)* cf. *paraleidyi* Mitchell; Tasch, p. 83, pl. 24, fig. 4.
1987 *Leaia (Hemicycloleaia) pincombei* Mitchell; Tasch, p. 122, 123, pl. 40, fig. 4.
1987 *Leaia (Hemicycloleaia) sulcata* (Kobayashi); Tasch, p. 127, pl. 41, fig. 3.
1987 *Leaia (Hemicycloleaia) oblongoidea* Tasch, p. 83, 124, pl. 24, fig. 1, pl. 40, fig. 8.
1987 *Leaia (Hemicycloleaia) belmontensis* Mitchell; Tasch, p. 79, pl. 22, fig. 2.
1987 *Leaia (Hemicycloleaia) immitchelli* Tasch, p. 80, 81, pl. 23, fig. 2.
1987 *Leaia (Hemicycloleaia) kahibahensis* Tasch, p. 81, pl. 24, fig. 3.
1987 *Leaia (Hemicycloleaia) magnumelliptica* Tasch, p. 81, 82, pl. 22, fig. 5.

Diagnosis. Carapace moderate to large in size and subovate in outline. 4.2–8.0 mm in length, 3.0–5.8 mm in height. Anterior radial carina slightly arcuate, posterior radial carina long and straight, both reaching to or near the ventral margin of the valve. Dorsal margin thickened into a third carina. Sometimes a short embryonic carina (see arrow, Fig. 7a,h), which is not present on all specimens of this species, originates near the dorsal margin slightly beyond the main posterior carina and deviates slightly from the dorsal margin.

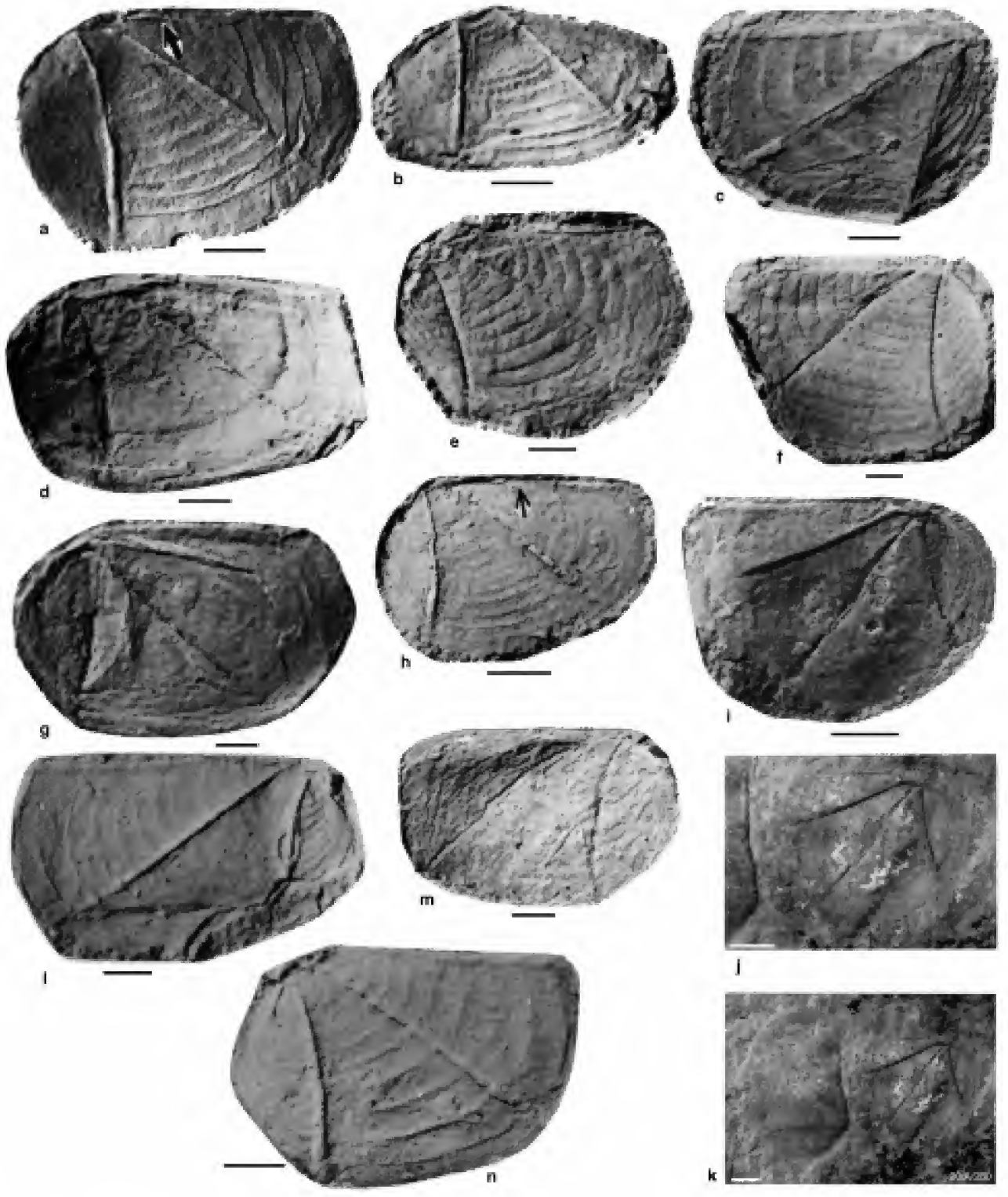

Figure 7. PERMIAN LEAIIDS, scale 1 mm. **a–n** *Hemicycloleaia mitchelli* (Etheridge): a—F 25459 (formerly *Leaia intermediata* Mitchell), internal mould of left valve; b—F 25463 (formerly *Leaia elliptica* Mitchell), internal mould of left valve; c—F 25421 (formerly *Leaia collinsi* Mitchell) internal mould of right valve; d—F 25461 (formerly *Trileaia sulcata* Kobayashi), external mould of right valve; e—F 25449 (formerly *Leaia pincombei* Mitchell) external mould of right valve; f—F 25426, external mould of left valve; g—F 25427 (formerly *Trileaia etheridgei* Kobayashi), external mould of right valve; h—holotype F 25487, internal mould of left valve, arrow points to embryonic rib sometimes present; i–k—F 25429 (formerly *Leaia belmontensis* Mitchell), external mould of a left valve overlies a fragment of an underlying valve, showing an associated complete right valve with only two major radial… [continued]

Growth bands broad and flattened, 10–17 in number. Umbo, small or moderate in size; two main radial carinae cross it, but do not converge on this area.

Remarks. Tasch (1987) proposed one new species, *Leaia (Leaia) oblongoidea* (pl. 24, fig. 1; pl. 40, fig. 8), based on an incomplete carapace. This species is obviously invalid for two reasons. First is a confusion over catalogue numbers in the plate explanation (Tasch, 1987, pl. 40) where F 25423 is given for *Leaia (Leaia) oblonga* (fig. 7) and F 25420 is given for *L. (Leaia) oblongoidea* (fig. 8). This is incorrect and the catalogue numbers should be reversed. Secondly, there is a discrepancy between pages 83 and 124 of Tasch's citations of Mitchell's plate and figure references. The synonymy given on page 83 for *oblongoidea* is incorrect, and should be reversed i.e., *L. (Leaia) oblongoidea* = *Leaia oblonga* Mitchell, 1925 (p. 441, pl. 41, fig. 5 *non* pl. 43, fig. 18). Finally, on page 124 there is an error (possibly typographic) in the citation of *L. oblonga* Mitchell, p. 441, pl. 41, fig. 3. Plate 41, fig. 3 refers to *L. intermediata* Mitchell; presumably Tasch meant plate 41, fig. 5, which illustrates the syntype (F 25420) of *L. oblonga.*

From our re-examination of Mitchell's type species in the Australian Museum, Sydney, all 16 of the above-mentioned species can be divided into two groups according to their configuration of carapace valve: the subovate form including *Leaia mitchelli, L. collinsi, L. elliptica, L. etheridgei, L. oblonga, L. oblongoidea, L. ovata, L. paraleidyi, L. pincombei, L. (H.) immitchelli, L. (H.) kahibahensis* and *L. (H.) magnumelliptica*; the subcircular form including *L. discoidea, L. compta, L. latissima, L. quadrata* and *L. quadriradiata*. Previously Tasch (1987) referred *Trileaia belmontensis* (Kobayashi) and *Leaia intermediata* to *L. (H.) mitchelli*, because there is no third main radial carina on the valve, except the dorsal carina for *belmontensis*. This incorrect understanding (Kobayashi, 1954) was due to another overlapping valve, and the new photograph in the present paper (Fig. 7k) shows that an associated valve with the holotype (F 25429) has only two main radial carinae. In the same monograph Tasch also referred *L. quadriradiata* to *L. (H.) mitchelli*. For all Mitchell's type specimens of subovate form, the two main radial carinae start from the umbo area and reach to or near the ventral margin of the valve, but the anterior radial carina of *L. quadriradiata* fades out above the ventral margin (Fig. 8f,h). This character is very similar in *L. discoidea* (Fig. 8f,h), and therefore it should be transferred from *L. mitchelli* to the subcircular form. Mitchell (1925) noted that there are two short embryonic ribs near the dorsal margin in "*quadriradiata*", a character used by Novozhilov (1952) and Kobayashi (1954) to introduce their respective genera *Brachioleaia* and *Quadrileaia*. However, the presence of embryonic ribs, as in "*mitchelli*" is an unstable character, and does not merit taxonomic recognition (Tasch, 1987).

A revised list of plate explanations in Tasch's (1987) monograph concerning Mitchell's type material is provided as an appendix to this paper.

Type locality and horizon. Chert Quarry near Belmont, NSW (Mitchell, 1925); Upper Permian Boolaroo Formation.

Hemicycloleaia discoidea (Mitchell, 1925)

Fig. 8a–d,f,h

1925 *Leaia discoidea* Mitchell, p. 441, pl. 41, fig. 6, pl. 43, fig. 22.
1925 *Leaia compta* Mitchell, p. 444–445, pl. 42, fig. 14.
1925 *Leaia latissima* Mitchell, p. 444, pl. 42, fig. 11.
1925 *Leaia quadriradiata* Mitchell, p. 441–442, pl. 41, fig. 7.
1952 *Cycloleaia discoidea* (Mitchell); Novozhilov, p. 1361–1371, fig. 2a. (= drawing of Mitchell, 1925, pl. 41, fig. 6).
1952 *Brachioleaia quadriradiata* (Mitchell); Novozhilov, p. 1372, fig. 3v (= drawing of Mitchell, 1925, pl. 41, fig. 7).
1954 *Discoleaia discoidea* (Mitchell); Kobayashi, p. 108, 109, 141, 156.
1954 *Discoleaia discoidalis* [sic] (Mitchell); Kobayashi, p. 142, text-fig. 30f (= drawing of Mitchell, 1925, pl. 43, fig. 22).
1954 *Leaia compta* Mitchell; Kobayashi, p. 108, 155.
1954 *Leaia latissima* Mitchell; Kobayashi, p. 31, 108, 109,159.
1954 *Quadrileaia quadriradiata* (Mitchell); Kobayashi, p. 108, 109, 144, 164, text-fig. 30k. (= drawing of Mitchell, 1925, pl. 41, fig. 7).
1956 *Hemicycloleaia compta* (Mitchell); Novozhilov, p. 32, pl. 4, figs. 5–7 (= Mitchell, 1925, pl. 42, fig. 14).
1956 *Cycloleaia discoidea* (Mitchell); Novozhilov, p. 78, pl. 14, fig. 2 (= Mitchell, 1925, p. 441, pl. 41, fig. 6).
1956 *Cycloleaia cyclica* Novozhilov, p. 78, pl. 14, fig. 3 (= *Leaia discoidea* Mitchell, 1925, pl. 43, fig. 22).
1956 *Brachioleaia quadriradiata* (Mitchell); Novozhilov, p. 75, pl. 13, fig. 5 (= Mitchell, 1925: 441–442, pl. 41, fig. 7).
1958 *Cycloleaia discoidea* (Mitchell); Novozhilov, Tasch, p. 1100.
1987 *Cycloleaia discoidea* (Mitchell); Novozhilov, Tasch, p. 79, 123, pl. 22, fig. 1, pl. 40, fig. 6.
1987 *Leaia (Hemicycloleaia) compta* Mitchell; Tasch, p. 126, pl. 41, fig. 5.
1987 *Leaia (Hemicycloleaia)* cf. *compta* Mitchell; Tasch, p. 80, pl. 22, fig. 4.
1987 *Leaia (Hemicycloleaia) latissima* Mitchell; Tasch, p.125, pl. 41, fig. 2.
1987 *Leaia (Hemicycloleaia) mitchelli* (?) Etheridge; Tasch, p. 121, pl. 40, fig. 5.

Lectotype. External mould of left valve (F 25419) described by Mitchell (1925: 441, pl. 43, fig. 22); by subsequent designation in Kobayashi (1954: 143) [*non* Tasch, 1987: 123].

[Figure 7, continued]... carinae and a dorsal carina; l—F 25420 (formerly *Leaia oblonga* Mitchell), internal mould of an incomplete right valve; m—F 25456 (formerly *Leaia ovata* Mitchell), external mould of left valve; n—F 25454 (formerly *Leaia paraleidyi* Mitchell), internal mould of left valve. All specimens are from the Upper Permian Boolaroo Formation of the Newcastle Coal Measures, Sydney Basin, NSW. In this figure a–i, l–n reproduced from Fossil Conchostraca of the Southern Hemisphere and Continental Drift; Paleontology, Biostratigraphy and Dispersal by P. Tasch (1987), *Geological Society of America Memoir* 165; used by permission of the Geological Society of America.

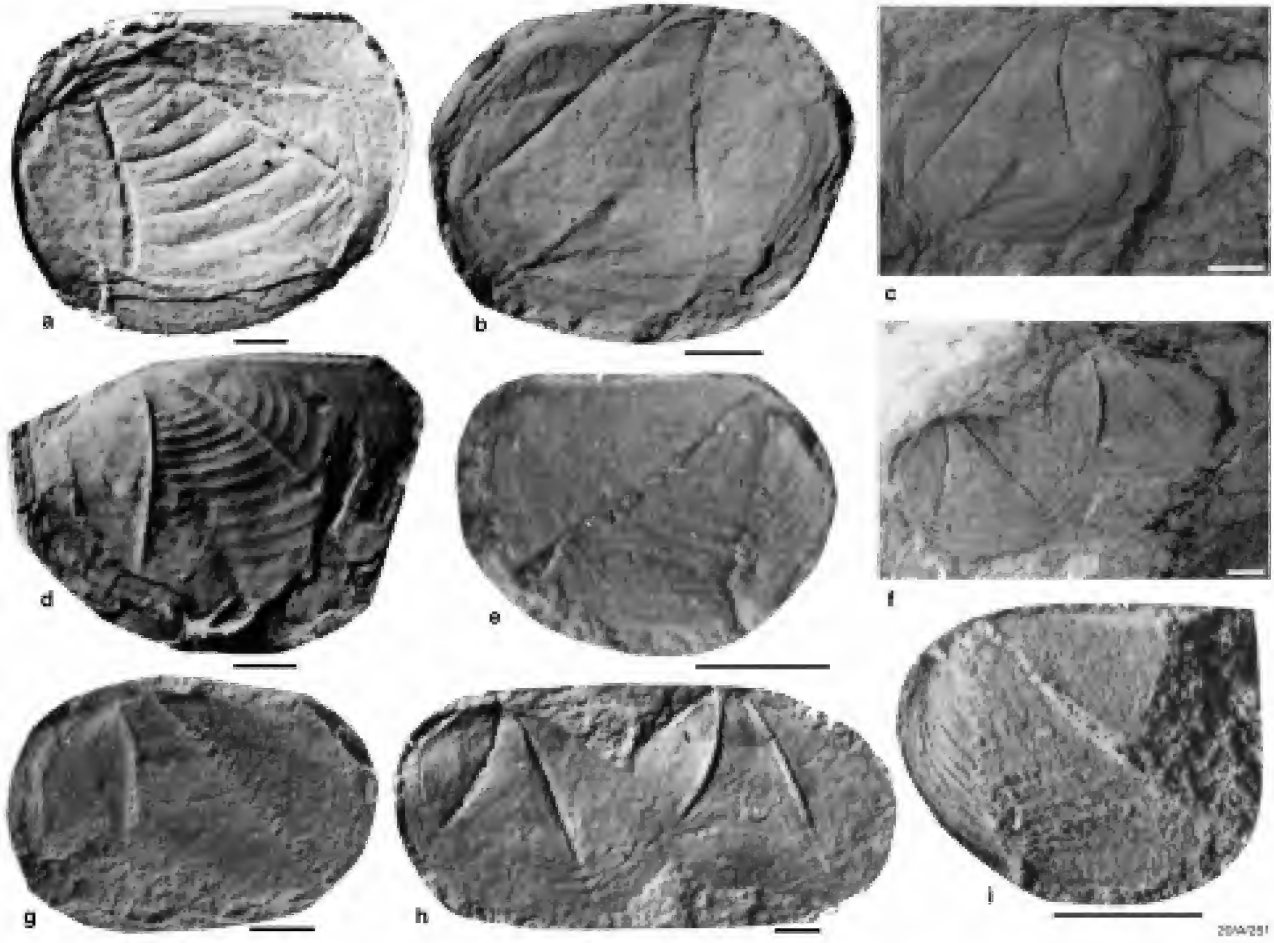

Figure 8. PERMIAN LEAIIDS, scale 1 mm. **a–d,f,h** *Hemicycloleaia discoidea* (Mitchell): a—F 25466 (formerly *Leaia latissima* Mitchell), external mould of right valve; b—lectotype F 25419, external mould of left valve; c—new photograph; d—F 25424 (formerly *Leaia compta* Mitchell), internal mould of left valve; f,h—F 25465 (formerly *Leaia quadriradiata* Mitchell), external mould of right valve on the left side and internal mould of left valve on the right side. Specimens from the Upper Permian Boolaroo Formation of the Newcastle Coal Measures, Sydney Basin, NSW. **e,g,i** *Hemicycloleaia deflectomarginis* (Tasch): e—holotype CPC 17173B, external mould of left valve; g—CPC 17174, (formerly *Leaia (H.)* sp. indet. 1 Tasch), internal mould of left valve; i—CPC 17173A, internal mould of holotype. Specimens from 4.2 km SSW of Winchester Homestead, Clermont, Bowen Basin, Blackwater Group. In this figure a,b,d and h are reproduced from Fossil Conchostraca of the Southern Hemisphere and Continental Drift; Paleontology, Biostratigraphy and Dispersal by P. Tasch (1987), *Geological Society of America Memoir* 165; used by permission of the Geological Society of America.

Diagnosis. Carapace moderate to large, subsemicircular or subcircular in outline, 4.2–8.0 mm long, 3.0–6.5 mm high. Growth bands broad and flattened, about 15 in number. Anterior radial carina gently curved and fades out above the ventral margin of valve. Posterior radial carina slightly straight and reaches near the ventral margin; both cross the umbo but do not meet. Sometimes the umbo is rather prominent (Fig. 8d). Dorsal margin frequently thickened to a thin carina. Rare occurrence of two short embryonic ribs near the dorsal margin and umbo area (Fig. 8f,h).

Remarks. Novozhilov (1952) proposed the genus *Cycloleaia* based on one of the two syntypes of *Leaia discoidea* Mitchell (1925: 441, pl. 41, fig. 6). Tasch (1987: 123) claimed that this specimen "has been lost and is no longer available for reference". The specimen (F 25422), however, has been studied by the present authors. Kobayashi (1954: 143) by subsequent designation, selected the second syntype (F 25419) figured by Mitchell (1925, pl. 43, fig. 22) as the holotype [sic] of *Leaia discoidea*, which he used as the type species for *Discoleaia*. As Novozhilov (1956) later introduced *Cycloleaia cyclica* based on this specimen (F 25419), the name of this species becomes an objective junior synonym of *Hemicycloleaia discoidea*.

The features of both syntypes (F 25419, F 25422) are very similar to *Hemicycloleaia mitchelli* except for the

growth lines, which Novozhilov (1956) considered to be obscure or absent. According to Tasch (1987) and from our examination, the syntype (F 25422) designated the holotype, is a poorly preserved specimen of an external mould of the left valve, with about 15 growth bands. Thus, we regard *Cycloleaia* Novozhilov, 1952 as a junior synonym of *Hemicycloleaia* Raymond, 1946.

Mitchell (1925) also described three other species of *Leaia* having a subcircular or subsemicircular carapace with two major radial carinae, of which the anterior one fades out above the ventral margin. They are *L. compta, L. latissima* and *L. quadriradiata*, which on the basis of page priority in his paper, we regard as synonyms of *Hemicycloleaia discoidea*.

This species differs from *H. mitchelli* only in the configuration of the carapace valve. It is very similar to the two, previously discussed, species of *Hemicycloleaia* from the Early Carboniferous of the Canning Basin. *Hemicycloleaia mitchelli* and *H. discoidea* might be regarded as dimorphs within a single population, but their carapaces are larger, and their growth bands are broader, but reduced in number, when compared to the Early Carboniferous taxa.

Type locality and horizon. Chert Quarries near Belmont, NSW (Mitchell, 1925); Upper Permian Boolaroo Formation.

Other locality. Merewether Beach; from just above Dirty Seam (Mitchell, 1925); Upper Permian Lambton Formation.

Hemicycloleaia deflectomarginis (Tasch, 1979)

Fig. 8e,g,i

1979 *Leaia (Hemicycloleaia) deflectomarginis* Tasch, p. 40, pl. 6, figs. 1,2.
1979 *Leaia (Hemicycloleaia)* sp. indet. 1, Tasch, p. 40, pl. 6, fig. 3.
1987 *Leaia (Hemicycloleaia) deflectomarginis*; Tasch, p. 85.
1987 *Leaia (Hemicycloleaia)* sp.; Tasch, p. 85.

Diagnosis. Carapace small to moderate size, subovate in outline. 2.9–6.1 mm long, 2.0–3.2 mm high. Anterior radial carina slightly curved, posterior radial carina straight, both reaching the ventral margin; dorsal margin not thickened into a carina. 10–13 or more growth bands.

Remarks. Tasch (1979) described three leaiid specimens from the Late Permian of the Bowen Basin, Queensland as *Leaia (Hemicycloleaia) deflectomarginis* and *Leaia (Hemicycloleaia)* sp. indet. Of these specimens, one (CPC 17173B) is the external mould of another (CPC 17173A), and there are no perceptible taxonomic differences between these and the one referred to *Leaia (Hemicycloleaia)* sp. indet. (CPC 17174). This single species differs from *H. mitchelli* and *H. discoidea* in having a smaller carapace, narrower growth bands, and especially the lack of a dorsal carina.

Type locality and horizon. 4.2 km SSE of Winchester Homestead, Clermont area, Bowen Basin, Queensland. Upper Permian Blackwater Group (topmost Fort Cooper Coal Measures).

Family **Rostroleaiidae** Novozhilov, 1956

[*Nom. transl.* Shen, 1978; *ex* Rostrolealinae Novozhilov, 1956]

Diagnosis. Leaioidea with posterodorsally recurved growth bands along dorsal margin, and one to five radial carinae.

Genus ***Rostroleaia*** Novozhilov, 1952

1952 *Rostroleaia* Novozhilov
1954 *Falsirostria* Novozhilov
1954 *Granirostria* Novozhilov
1969 *Rostroleaia* Novozhilov; Tasch
1976 *Rostroleaia* Novozhilov; Zhang, Chen & Shen
1979 *Rostroleaia* Novozhilov; Tasch & Jones
1985 *Rostroleaia* Novozhilov; Chen & Shen
1987 *Rostroleaia* Novozhilov; Tasch

Type species. *Rostroleaia martynovae* Novozhilov, 1952: 369, fig. 1 (by original designation); Upper Permian (Kazanian), Nikolaevsk Gorge, Kargaline Mine, Ural Mountain Region, at the boundary with the Kungurian.

Diagnosis. Rostroleaiidae with elliptical carapace and two radial carinae. The dorsal margin thickened into a third carina. Growth bands gently recurved near the dorsal margin in the posterodorsal sector or this sector prolonged sharply.

Range. Middle Devonian to Upper Permian.

Distribution. China, Russia, England, USA and Australia.

Rostroleaia carboniferae (Tasch, 1979)

Fig. 6j–o

1979 *Limnadiopsileaia carboniferae* Tasch, p. 14, pl. 2, figs. 6–8.
1979 *Rostroleaia* sp. Tasch, p. 14, pl. 2, fig. 5.
1987 *Limnadiopsileaia carbonifera* [sic]; Tasch, p. 79.
1987 *Rostroleaia* sp.; Tasch, p. 79.

Diagnosis. Carapace small, elliptical to ovate in outline, with two radial carinae. Dorsal margin thickened into a third carina and posterior growth lines gently recurved in the posterodorsal sector (Fig. 6l,o). Growth bands broad and flattened, about 15 in number.

Topotype. Left valve and its external mould (CPC 33823) taken from the original collection, but not from the type series.

Remarks. This species was first assigned to *Limnadiopsileaia*, a genus based on a species the holotype of which is characterised by a single posterior radial carina. Its holotype (CPC 17141, Fig. 6k,l) is a broken left valve. Because the anterodorsal part of the external mould of its right valve exposes an anterior radial carina (Fig. 6k), we transfer this species to *Rostroleaia*. This reassignment is supported by evidence from a specimen (CPC 33823; Fig. 6m–o) selected from the original collection in AGSO.

Type locality and horizon. Grant Range No. 1 Well, core 52 (7907–7912 feet); Lower Carboniferous Anderson Formation.

Biostratigraphic implications of Australian Leaioidea faunas

Early Carboniferous Leaioidea

In the Canning Basin, *Hemicycloleaia andersonae* (Tasch, 1979), *H. grantrangicus* (Tasch, 1979) and *Rostroleaia carboniferae* (Tasch, 1979) are found only in Grant Range No. 1 Well (Fig. 3), where they are distributed over an interval of 192 m (7907–8537 feet) at the top of the Anderson Formation. Öpik (in McWhae *et al.*, 1958) regarded this *Hemicycloleaia* sequence as Late Carboniferous (Westphalian–early Stephanian) in age, but older occurrences of this genus are known. Copeland (1957) showed that *Hemicycloleaia* of the *tricarinata* species-group is present in the Namurian of eastern Canada. Also, *H. grantrangicus* is present in the Drummond Basin, Queensland, in the Raymond Formation, which is early Viséan, possibly late Tournaisian in age (this paper). In palynostratigraphic terms, the type interval is within the *Grandispora maculosa* Assemblage (Kemp *et al.*, 1977), as identified by C.B. Foster (pers. comm.) in core 64 (8544–8554 feet), and reported by Playford & Powis (1979) in core 50 (7502–7505 feet) and core 48 (7101–7103 feet). The *G. maculosa* Assemblage is apparently as old as middle Viséan in New South Wales, and as young as earliest Namurian in the Bonaparte Basin of northwestern Australia (Roberts *et al.*, 1995; Jones, 1996). Below core 62 (8530–8536 feet) is a thick interval (3324 feet; 1013 m) apparently barren of conchostracans. *Hemicycloleaia* was recorded (J.G. Tomlinson, unpublished BMR file report, 6 October 1955) from cuttings taken from 11860–12000 feet, and although some downhole contamination is possible, we consider that recirculation of cuttings over such a thick interval, more than 1000 m, is highly unlikely. Thus, two distinct leaioid intervals are in the well. Both are preceded by marine limestone incursions; at 12590 feet (with brachiopod or bivalve impressions and crinoid ossicles), and 9788–9808 feet (core 72; with conodonts, including *Cavusgnathus* sp.; ostracods, including *Cavellina* spp., *Lichvinella* sp., *Paraparchites* sp.; eridostracans *Cryptophyllus* sp. B Jones, and bivalves). The younger marine incursion is also recognised in other wells e.g., Yulleroo 1 (2840–2890 feet; with conodonts *Cavusgnathus unicornis, Spathognathodus scitulus*, ostracods, and eridostracans *Cryptophyllus* sp. B Jones), and Barlee 1 (core 2, 2308–2325 feet) with conodonts (*Ozarkodina*-element), ostracods, and eridostracans (*Cryptophyllus* sp. B Jones). No ostracods were found in association with the conchostracan samples. We conclude that (i) the possible age range of the upper leaioid fauna is middle Viséan to early Namurian, and (ii) the first (early Viséan) appearance of *Hemicycloleaia* in Grant Range 1 is compatible in age with the presence of *Hemicycloleaia grantrangicus* in the Raymond Formation (?late Tournaisian to early Viséan) of the Drummond Basin.

Late Permian Leaioidea

Foster & Jones (1994) concluded that the use of conchostracan species for precise correlation within the Late Permian, is inhibited by insufficient detailed knowledge of their stratigraphic ranges and geographic distribution. Despite the inclusion of many of Mitchell's (1925, 1927) leaiid and "estheriid" species in faunal lists for the Tatarian of the Russian Platform (e.g., Olferev, 1974; Kozur, 1977; Molostovskaya, 1997), to our knowledge none have been figured. From the Russian literature available to us, we know of no published descriptions of leaioid species from the type Tatarian (*Triedrolophus tverdochlebovi* Molin, 1968 from the lower Tatarian is now excluded from the Leaioidea; Chen & Shen, 1985).

However, those of Mitchell's (1925) leaiid species figured and described by Novozhilov from the Lower Tungus Basin, northern Siberia, warrant further discussion. In addition, some of Mitchell's (1927) "estheriid" species figured and described by Novozhilov from the Lower Tungus and Nordvik Basins also merit consideration. Thus, our work suggests that some broad correlations can still be made, and confirms, in part, Novozhilov's (1970) correlation of the upper NCM (Belmont Series [sic]) with the Upper Tatarian.

Lower Tungus Basin (Fig. 9): The Late Permian conchostracans from the Newcastle Coal Measures (NCM) compare well to those described (Novozhilov, 1965) from the pyroclastic Korvunchan Series in the Lower Tungus Basin (Fig. 8). *Hemicycloleaia mitchelli* (Etheridge, 1892) is present in the lower part of the Bugariktin Suite, near the top of the Korvunchan Series, and was figured and referred by Novozhilov (1965) to the synonyms *Mimoleaia mitchelli* (Etheridge, 1892) Novozhilov, 1954 and *Leaianella paraleidyi* (Mitchell, 1925). The figured specimens (see synonymy list p. 233) appear to be the only ones to our knowledge that illustrate *Hemicycloleaia mitchelli* from the Former Soviet Union. *Mimoleaia belozerovi* Novozhilov, 1965 (pl. 7, figs. 1–4) is possibly synonymous with *H. mitchelli*. The only other leaiid species in the NCM, *H. discoidea* (Mitchell, 1925), may be present in the Bugariktin figured by Novozhilov (1965, text-fig. 70, and pl. 7, fig. 7) under the name *Brachioleaia? quadriradiata* (Mitchell, 1925). The lower part of the Bugariktin Suite also contains, amongst others, two estheriid taxa described by Mitchell (1927) from the NCM viz., *Palaeolimnadia glabra* [recorded as *L. (Limnadia) glabra*], and *Cyzicus (Euestheria) novocastrensis* [recorded as *Pseudestheria novocastrensis*] (Novozhilov, 1958, 1965, 1970). Other estheriid taxa were collected from lower in the Korvunchan Series from strata thought to belong to the Tutonchan Suite. These were listed by Novozhilov (1965: 45) as Mitchell's (1927) species *Pseudestheria obliqua, P. novacastrensis, P. linguiformis*, and *P. trigonellaris*. The host strata, however,

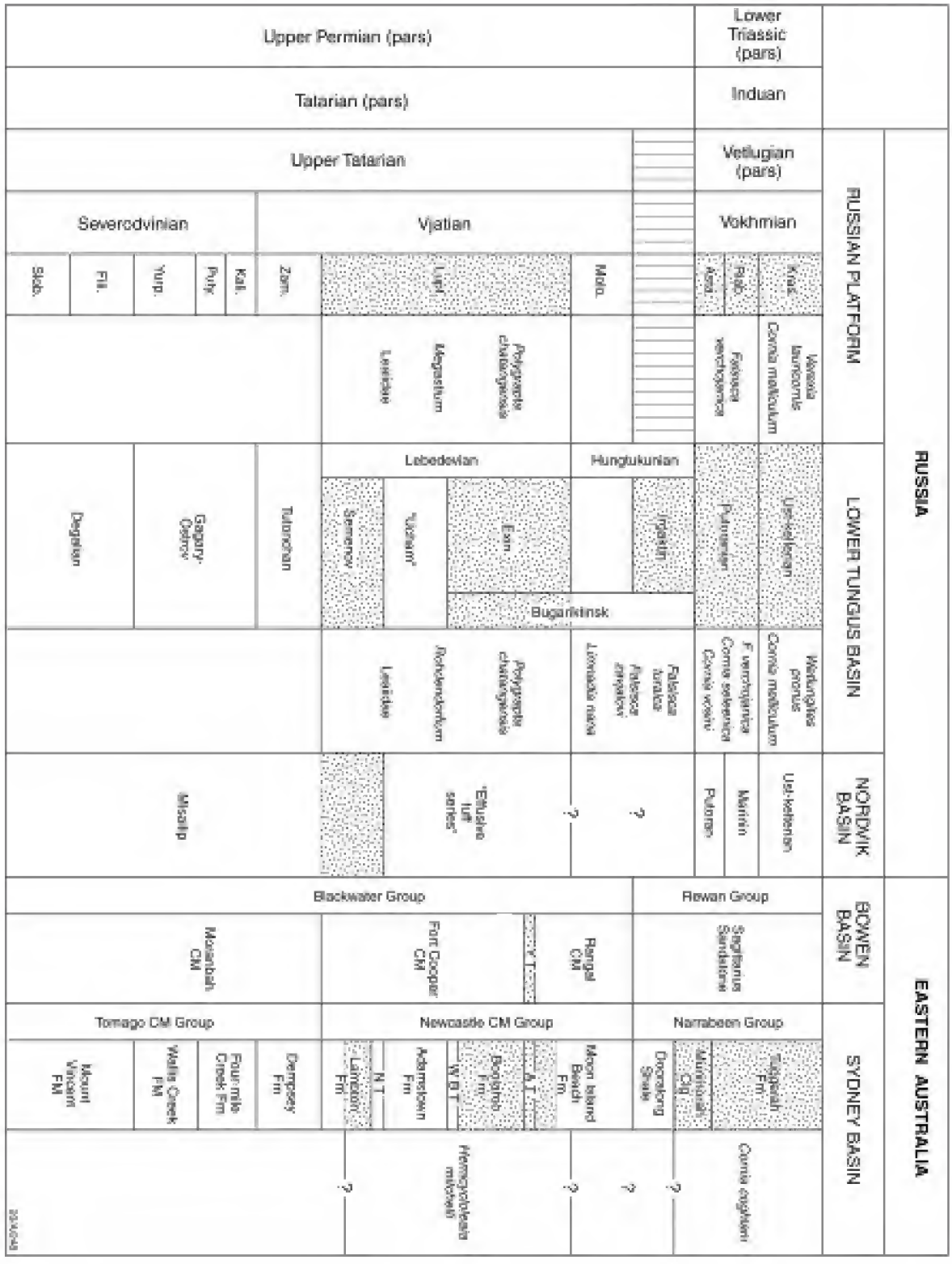

Figure 9. Correlation of the Upper Permian and lowest Triassic rocks of the Russian Platform, the Siberian Platform, and eastern Australia, based on Conchostraca. Russian data from Lozovsky, 1998. Stippled areas indicate sequences with conchostracan faunas. Abbreviations: members of Vokhmian horizon = Kras. (Krasnobakovian), Riab. (Riabinian), Asta. (Astashichian); members of Vjatian horizon = Molo. (Molomian), Lupt. (Luptugian), Zam. (Zamoshian); members of Severodvinian horizon = Kali. (Kalininian), Puty. (Putyatian), Yurp. (Yurpalovian), Fili. (Filian), Slob. (Slobobian). Abbreviation of names of tuff beds in eastern Australia: Bowen Basin, YT = Yarrabee Tuff; Sydney Basin, AT = Awaba Tuff (Formation), NT = Nobbys Tuff (Formation), WBT = Warner Bay Tuff (Formation).

are now known to be younger than authentic Tutonchan (Sadovnikov & Orlova, 1990, 1993; see below).

The stratigraphic nomenclature used by Novozhilov (1965, 1970), for the Korvunchan (Tuffogenic) Series, and followed above, has now been revised on the basis of megafloral, palynological and conchostracan studies (Gomankov & Meyen, 1986; Sadovnikov, 1997; Sadovnikov & Orlova, 1990, 1993, 1995; Orlova, 1990). Furthermore, new data on the field relationships of the Korvunchan (Tuffogenic) Series and the overlying Siberian Traps (Lozovsky, 1997, 1998), and geochronological studies of the Siberian Traps (Renne & Basu, 1991; Renne *et al.*, 1995; Kamo *et al.*, 1996), and the proposed Permian/Triassic boundary stratotype at Meishan, China, (Claoué-Long *et al.*, 1991, 1995; Renne *et al.*, 1995; Bowring *et al.*, 1998), have contributed to an improved understanding of the stratigraphic position of the Korvunchan conchostracans.

Correlation between the Lower Tungus Basin and the Russian Platform (Fig. 9): Sadovnikov & Orlova (1993) suggested on floral evidence, a correlation between the Gargaryostrov horizon, at the base of the Korvunchan Series, with the lower Upper Tatarian (Severodvinian). The overlying Tutonchan horizon is devoid of conchostracans, and is correlated by these authors to the uppermost Tatarian (Vyatian). The post-Tutonchan succession includes the Lebedevian horizon, the lower part of which contains the non-leaioid taxa listed above. These taxa previously thought by Novozhilov (1965: 45) to have come from the Tutonchan, were probably collected from the Semenov and Dyukin beds. The Exin beds of the uppermost Lebedevian horizon correspond to the lower part of the Bugariktin Suite which hosts the *Hemicycloleaia mitchelli* and non-leaioid fauna described by Novozhilov (1958, 1965, 1970). This conchostracan fauna extends upwards into the overlying Hungtukunian horizon of the Bugariktin Suite (Sadovnikov, 1997), and is replaced by a fauna dominated by *Falsisca turanica* (Novozhilov, 1965) in the upper part of the Bugariktin Suite (Irgaktin beds), at the base of the Putoranian Series (horizon). The overlying Nidym Suite in the lower Putoranian can be correlated with the Morongov suite of lavas at the base of the Upper Norilsk basalt (Lozovsky, 1997, 1998). As the minimum U-Pb age of the Morongov suite (251.2±0.3 Ma; Kamo *et al.*, 1996) is within analytical error of the proposed Permian/Triassic boundary stratotype at Meishan, China, for U-Pb ages of zircon (251.1±3.6 Ma, Claoué-Long *et al.*, 1991, 1995; 251.4±0.3 Ma, Bowring *et al.*, 1998) and for a 40Ar/39Ar age of sanidine (249.9±1.5 Ma, Renne *et al.*, 1995), it is reasonable to accept a Permian age for the Korvunchan conchostracans, because they are stratigraphically older than the inception of the Siberian Traps.

The floral evidence for the Sadovnikov & Orlova (1993) correlation mentioned above i.e., the Gargaryostrov horizon with the Severodvinian, and the Tutonchan horizon with the Vyatian, implies that the overlying Korvunchan leaioid fauna is either early Vyatian (Novozhilov, 1970) or possibly post-Tatarian, pre-Vetlugian (Sadovnikov & Orlova, 1993) in age. Sadovnikov (1997) and Sadovnikov & Orlova (1994, 1995) regarded the Lebedevian, Hungtukunian and Putoranian horizons to correspond to the hiatus between the Tatarian Stage and the Lower Triassic Velugian Stage of the Russian Platform, for which they proposed the Taimyrian Stage. However, on palynological evidence, this hiatus is probably much shorter than that envisaged by Sadovnikov & Orlova, and may be equivalent to the Hungtukunian only, as this horizon contains the *Triquitrites proratus* spore assemblage, which is absent from the Vyatian of the Russian Platform, but present in the upper Zechstein (Z6, Z7) of the German Basin (Yaroshenko, 1990), and is represented by the *Leiosphaeridea changxingensis-Micrhystridium stellatum* Assemblage Zone in the uppermost Changhsingian at Meishan, South China (Ouyang & Utting, 1990). This stratigraphic link is an important part of the correlation proposed by Lozovsky (1997, 1998), which is adopted in this paper (Fig. 6).

Nordvik Basin (Fig. 9): The conchostracan fauna at the top of the subsurface Misailap Series (Novozhilov, 1958) includes Mitchell's species *Palaeolimnadia glabra, Cyzicus (Euestheria) novocastrensis, C. (E.) obliqua*, and *Glyptoasmussia belmontensis*. This fauna is probably equivalent to the post-Tutonchan fauna [*Cyzicus (Euestheria) linguiformis, C. (E.) novacastrensis, C. (E.) obliqua* and *C. (E.) trigonellaris*] that was probably collected from younger (Semenov and Dyukin) beds in the lower part of the Lebedevian horizon in the Lower Tungus Basin (Sadovnikov & Orlova, 1990, 1993). Of these Mitchell (1927) species, *Cyzicus (Euestheria) novacastrensis* has been reported from the Severodvinian horizon of the Upper Tatarian stratotype sections of the Russian Platform (Olferev, 1974).

Correlation between the Nordvik Basin and the Russian Platform (Fig. 9): Lev (1957) correlated the non-marine ostracods (mostly new species of *Paleodarwinula*) from the *Darwinula arctica* beds of the Misailap and the overlying Effusive-Tuff Suite, with the Urzhum horizon (Early Tatarian) and the lowermost part of the Severodvinian horizon (earliest Late Tatarian) of the Russian Platform. This correlation is slightly older than the one advocated here, and suggests that the fauna needs to be redescribed. Pollen studied from the same deposits by Dibner (1958) were correlated with other Angaran assemblages regarded as Tatarian. However, it is uncertain whether these Angaran assemblages can be correlated with those of the type Tatarian of the Russian Platform (Gomankov & Meyen, 1986). Moreover, even in the northern Russian Plate there is still doubt about the palynological placement of the Kazanian-Tatarian boundary (Astafurov & Medvedeva, 1993).

Late Permian correlation between the Sydney Basin and the Lower Tungus and Nordvik Basins, northern Siberia (Fig. 9)

The presence of *Hemicycloleaia mitchelli, H. discoidea* and the estheriid species *Palaeolimnadia glabra* and *Pseudestheria novocastrensis* in the Belmont localities in the upper part of the NCM (Boolaroo Formation) indicates a correlation with these taxa described by Novozhilov from

the lower part of the Bugariktin Suite (= Exin beds, at the top the Lebedevian) of the Lower Tungus Basin. This comparison parallels the similarity between the Belmont insect fauna of the upper NCM and that of the Angara province (Riek, 1970).

The estheriid species *Cyzicus (Euestheria) linguiformis, C. (E.) novacastrensis, C. (E.) obliqua*, and *C. (E.) trigonellaris* in the Merewether Beach locality in the lower part of the NCM (Lambton Formation) can be correlated with those collected from the lower Lebedevian Semenov and Dyukin beds of the Lower Tungus Basin. Similarly, these species indicate a correlation with those from the subsurface Misailap Series in the Nordvik Basin (Novozhilov, 1958, 1965) described and figured as *Palaeolimnadia glabra, Cyzicus (Euestheria) novocastrensis, C. (E.) obliqua*, and *Glyptoasmussia belmontensis*.

In summary, the Late Permian leaioid and estheriid faunas of the Newcastle Coal Measures of the Sydney Basin are correlated with those of the Lebedevian of the Lower Tungus and Nordvik Basins, northern Siberia, which in turn, indicate a correlation with the Late Tatarian Vjatian (Luptug member) horizon of the Russian Platform (Lozovsky, 1998).

Molostovskaya (1997) listed *Hemicycloleaia intermediata*, and *Siberioleaia oblonga*, both junior synonyms of *Hemicycloleaia mitchelli*, in the Late Tatarian (Severodvinian) conchostracan fauna of the Russian Platform. If this is confirmed, and if the correlation presented here (Fig. 9) is correct, with further work, we would expect to find *H. mitchelli* within the Tomago Coal Measures.

The palaeobiogeographic distribution of Mitchell's (1925, 1927) Late Permian (Tatarian) conchostracan species in the Siberian Platform, Russian Platform, and eastern Australia requires an explanation. The Russian species could be different to those of Mitchell, but show an ecophenotypically similar carapace morphology, and reflect the bipolar distribution of cool waters at that time. Alternatively, if they are conspecific, the distribution of land and sea, according to current Late Permian palaeogeographic reconstructions (e.g., Erwin, 1994; Golonka *et al.*, 1994; Scotese & McKerrow, 1990), would have allowed migration to take place. Tasch (1987) envisaged a non-marine, interlacustrine dispersal, originally as wind-transported eggs, between the Siberian Platform, Russian Platform, and eastern Australia via China. We speculate, without necessarily extrapolating the lacustrine milieu of extant conchostracan species to Palaeozoic species, that they may have lived in estuaries and ephemeral relict water bodies along a coastal plain, where their eggs could be dispersed by wind, and by minor marine incursions. We find it difficult to exclude the possibility that marginal marine influences played some role, however minor, in the distribution of those of Mitchell's (1925, 1927) conchostracan "species" identified in the Late Permian of Russia (Novozhilov, 1956, 1965).

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Appendix

A revised list of plate explanations in Tasch's (1987) monograph concerning Mitchell's type material.

Page 228, pl. 40, fig. 2, the holotype of *Leaia mitchelli* Etheridge, is an internal mould of a left valve [not right valve]; fig. 3, the holotype of *Leaia collinsi* Mitchell is an internal mould of a right valve [not right valve]; fig. 5, length of valve of *Leaia quadriradiata* Mitchell is 4.2 mm [not 6.5 mm]; fig. 7 and 8, the catalogue number (F 25420 and F 25423) should be reversed.

Page 230, pl. 41, fig. 1, t, the holotype of *Leaia intermediata* Mitchell is an internal mould of left valve [not left valve]; fig. 4, the holotype of *Leaia belmontensis* Mitchell is an external mould of left valve [not external mould of right valve]; fig. 6, the holotype of *Trileaia etheridgei* Kobayashi is an external mould of right valve [not left valve]; fig. 7, the holotype of *Leaia elliptica* Mitchell is an internal mould of left valve [not external mould of left valve].

Page 232, pl. 42, fig. 8, the holotype of *Leaia paraleidyi* Mitchell is an internal mould of left valve.

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